DEMOGRAPHICS OF SELECTED CROCODILIAN POPULATIONS BASED UPON THE PATTERNS OF HARVEST, REPRODUCTION, AND SKULL MORPHOMETRY
CASE STUDIES FOR *Crocodylus novaeguineae*, *C. porosus*, AND *Alligator mississippiensis*

BY

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DEMOGRAPHICS OF SELECTED CROCODILIAN POPULATIONS BASED UPON THE PATTERNS OF HARVEST, REPRODUCTION, AND SKULL MORPHOMETRY: CASE STUDIES FOR *Crocodylus novaeguineae*, *C. porosus*, AND *Alligator mississippiensis*

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(Wildlife and Range Sciences)

Demographics of New Guinea (*Crocodylus novaeguineae*) and saltwater (*C. porosus*) crocodiles from Papua New Guinea (PNG) and American alligators (*Alligator mississippiensis*) from Florida and Louisiana, USA, were investigated between 1980-1987. Inferences were drawn based upon the patterns of harvest, reproduction, and skull morphometry for one or more of these species.

Legislated management of PNG crocodiles began in 1969. Nearly 450,000 crocodiles (80% *C. novaeguineae*) were harvested for commercial trade between 1969-1980. Compositions of *C. novaeguineae* and *C. porosus* harvests for 11 geographic areas are presented along with an overview of the industry and a discussion on limitations of this database.

The harvest patterns of PNG crocodiles are discussed based on analysis of the preceding. No trends in numerical harvest were found for either species, although some trends were detected in the frequency of harvest composition for *C. novaeguineae*. Harvest compositions strongly differed among populations for most within year intra-specific comparisons for each species. Despite being better protected by existing legislation with respect to adult size classes, *C. porosus* populations experienced far higher harvest mortality rates than *C. novaeguineae* populations.

Models are presented for the estimation of nesting female crocodilian size from clutch characteristics. The correlates of reproductive mode for *A. mississippiensis* (pulse model) and *C. novaeguineae* (flow model) as well as their harvest implications are discussed. Reproductively active female alligators from widely disjunct harvested populations were significantly smaller than those in a protected population where larger females may have precluded smaller females from nesting. Most of the nesting female crocodiles were smaller than the size protected by law and were thus exposed to harvest, which presumably led to a higher turnover rate of the breeding segment and a reduced production of hatchlings.

Ontogenetic variation in relative growth of the skull is quantified and described for C. novaeguineae. An assessment of its utility for the prediction of the sex and size of individuals is made. Allometric coefficients for estimation of size are given and models for gender prediction through parametric discriminant analysis or nonparametric binary tree classification methods are provided.

CHAPTER 1
PREFACE

The focus of this dissertation is on the demographics of selected tropical and temperate crocodilian populations based upon inferences drawn from several sources. These include (1) crocodile skin industry trade statistics and associated harvest patterns, (2) the comparative gross morphometry and reproductive mode of nesting female crocodilians, and (3) a quantitative analysis of relative growth of the crocodilian skull. Such rather diverse topics were selected to address separate, but little known, aspects of crocodilian population biology. In some respects they pose similar questions (i.e. - How to interpret size and sex structure of populations from unknown sex hides or skulls, or from clutch data where the parenting female remains unseen?), but researched from different methodologies. As such this will help assess how well each section complements or refutes the findings of each other and lends toward a holistic approach for the conservation and management of these resources. These studies stem from 30 months of fieldwork between 1980-1987 on three crocodilian species: 21 months in Papua New Guinea (PNG) working with New Guinea

(Crocodylus novaeguineae) and saltwater (C. porosus) crocodiles, plus nine months divided between Louisiana and Florida researching American alligators (Alligator mississippiensis).

In Chapter 2, I present a summary of the crocodile skin industry trade statistics for PNG from 1969-1980 and review some difficulties associated with its use. These years cover the period from the inception of legislated management of the crocodilian resource through various changes toward the development of the industry as it stood for what is the basis of present policy. Nearly 450,000 C. novaeguineae (roughly 80% of the harvest) and C. porosus were harvested during those years for which the annual species and size compositions of harvests from 11 geographic areas are presented. Data prior to 1969 are sparse and difficult to interpret, but they are also included and indicate that the total harvests were substantially greater during pre-management years. Most of these data were generated from obscure sources contained in dusty files that were not well safeguarded while continually shifted from one government department to another. By means of this chapter, a permanently accessible reference base is created for management and conservation authorities.

The synopses found in Chapter 2 serve as the database for analyses performed in Chapter 3, which deal with the observed harvest patterns and trends of those data. The data from Chapter 2 provide an indirect measure of size, but contain no information on the sex or age of individuals. In Chapter 3, I tackle the thorny problems of retrospectively assigning hide data to biologically meaningful size, sex, and age classes. These transformations are then used to derive harvest mortality rates on populations of each species to assess the impacts of harvesting on and among them. Limitations in the use of such data are discussed and areas for further research are suggested.

In Chapter 4, I investigate various relationships among gross morphometrics of nesting crocodilians and how these values may be indicative of observed reproductive output (clutch mass and clutch size). I also examine how known clutch parameters may be useful in predicting the sizes of unseen parenting female crocodilians and thus used to profile the nesting segments of breeding populations. Within this framework, I further explore the comparative reproductive modes of selected tropical and temperate crocodilians and discuss the harvest implications of these factors in relation to conservation strategies.

The subject of Chapter 5 is one that has hitherto received little attention--a quantitative analysis of relative growth patterns of the crocodilian skull. General ontogenetic trends of crocodilian cranial growth have been outlined by Mook (1921b), Kalin (1936, 1955), and Brongersma (1941). Subsequently, Iordansky (1973) developed cranial indices useful for interspecific comparisons of relative growth among the order Crocodylia. All these studies were limited by the lack of quantitative assessment of growth with respect to the size, sex, and age of individuals. A major advancement in this field occurred in the mid-1970's when Dodson (1975) explored the functional and ecological significance of relative skull growth within known size American alligators (A. mississippiensis). Here too, however, the relationships with the gender and age of individuals were not examined. In Chapter 5, I extend previous investigations on this subject area by including large data subsets from known gender animals from a species (C. novaeguineae) for which age classes are known or assigned. Analytical models are thereby developed to portray ontogenetic changes in relative skull growth of this crocodile from a multidimensional character framework. That knowledge is used to assess the utility of functional patterns of relative growth as a predictor of gender and age class.

Demographic parameters of crocodilian populations are often poorly understood or not known at all. The ability to monitor and interpret demographic trends of populations plays a key role in the establishment of conservation strategies and tactics. Knowledge gained from these studies will better enable conservation and management authorities to determine population structural parameters of crocodilian resources, be they subject to harvest or accorded full protection.

CHAPTER 2

CROCODILE SKIN INDUSTRY TRADE STATISTICS FOR PAPUA NEW GUINEA,1969-1980

Introduction

The crocodile skin industry has formed the basis for rural commerce throughout lowland areas of Papua New Guinea (PNG; Fig. 2-1) for several decades. This entails the exploitation of populations for both the New Guinea (*Crocodylus novaeguineae*) and saltwater (*C. porosus*) crocodiles. Although there is no closed season or limit on the number of crocodiles that may be taken, there are size restrictions on animals harvested for economic gain

Individuals engaged in the buying or exporting of crocodile products from PNG must be licensed by the Wildlife Division (Department of Lands, Surveys, and Environment) under terms of the 1966 Crocodile Trade (Protection) Act. Enacted in 1969, this law set an upper size limit of 20" (51 cm) commercial belly width on skin trafficking of both species to protect wild brood stocks. This restriction was repealed in the Sepik and Madang provinces from 1972 to early 1975, but was reinstated thereafter. Under terms of this Act buyers were required to submit quarterly return files on their purchases and exporters had to secure written

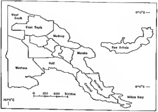

Figure 2-1. Map of Papua New Guinea indicating provinces of crocodile harvest mentioned in text, excluding Manus (2°5'S, 147°0'E), New Ireland (3°0'S, 151°30'E) and the North Solomons (6°0'S, 155°0'E). Right border of map is 153°E. Papuan Region provinces include, Western, Gulf, Central, and Milne Bay. The remaining labelled provinces are part of the New Guinea Region.

authorisation from the Wildlife Division prior to the export of any consignment of live crocodiles or crocodile skins. Additionally, all shipments of crocodilian products were made subject to inspection by enforcement officers.

Following the independence of PNG in September 1975, concern was expressed in restructuring the crocodile skin industry whereby national interests would be promoted over those of expatriates who had historically been the main beneficiaries of the trade. Toward this end, the Food and Agricultural Organisation of the United Nations (FAO) joined forces with the PNG government in 1977 to vitalise assistance for management of the industry. A major shift in the focus of the industry occurred in 1979 when a national buying scheme was established to encourage the sale of small live crocodiles to large scale commercial enterprises for rearing to counter the economic waste in the marketing of small size skins. Subsequent legislation led to the introduction of a minimum size skin limit of 7" (18 cm) belly width in February 1981. More detailed reviews of the history of crocodile exploitation in PNG and government policies toward this resource may be found elsewhere (Downes, 1971, 1973; Bolton, 1980; Bolton and Laufa, 1982; Hollands, 1987).

In 1980 I joined the FAO monitoring effort on biological investigations of PNG crocodiles and compiled harvest data on these species during 1980-1981. My initial review of the data base indicated major flaws in the collection and tabulation process since forms submitted by buyers and exporters were ill-suited for the compilation of biologically meaningful data and hence were left to accumulate. My objectives in presenting these data are twofold: (1) to provide a permanently accessible reference source of the trade statistics for management authorities and biologists involved in the crocodilian skin industry and (2) to illuminate the inherent difficulties encountered in compiling these data and explain how they were circumvented. Other factors not addressed herein, such as the conversion of commercial belly width measurements to more biologically meaningful units, size class sex ratios, and the assignment of size to age classes, are presented elsewhere along with an analysis of the harvest patterns exhibited by these data (CHAPTER 3).

Methods

Data Sources

Most data presented herein were tabulated from the export application records on file with the PNG Wildlife Division headquarters in Waigani, Port Moresby. The few remaining data are from published accounts, correspondence records on file at the Wildlife Division, or were obtained directly from trade sources. Raw data were compiled from every available approved application for each licensed exporter per calendar year from 1969 to 1980. Variables recorded were: exporter, date of application, origin of purchases, species, skin type (belly skin or hornback), skin size, and number of skins per size class. Additionally, several thousand small live crocodiles were purchased by government stations during 1979 and 1980 and resold to large scale commercial rearing farms. Records for that trade were obtained directly from government sources.

The inclusion of buyer quarterly returns as a data base was rejected on the grounds that the data format therein was not explicit and therefore, by and largely useless for monitoring purposes. Also, a very poor record of receipt and followup on those forms was evident. Even had those records been complete and up-to-date it would have been hopelessly confounded by the occurrence of one buyer reselling his stock to another buyer (rather than exporting directly) which would introduce an immeasurable factor of duplication.

A number of difficulties arose in the segregation and compilation of raw data. Such shortcomings, and the manners in which they were resolved, are outlined below.

Exporter Identification

Exporters who were licensed for trade in the crocodile skin industry during the years 1969-1980 are listed in Table

A-1, Appendix A. However, not all licensed individuals subsequently exported crocodile skins. Furthermore, examination of the then used exporters file registry (since revised) revealed a disturbing gap in the sequential order of licensing that left 20 license numbers unaccounted for. I presumed that those numbers were not in fact ever used except for being tentatively assigned to unknown applicants who later withdrew their applications or had them refused by the Management Authority. Additionally, some exporter files were discovered to be missing (part 1 of CE [Crocodile Exporter] 2, CE4, CE6 [part 1], CE7 [part 1], CE9, CE12, CE16 [part 1], and CE45 [part 1]) and never accounted for Of these missing files, three are known to contain the records for major hide industry exporters: CE2, CE4 (both Papua Region traders) plus a New Guinea Region trader, CE45. The years 1969 to 1972 are affected by their loss. Data for 1973 onward are believed to be a complete reflection of all legal exports.

Date of Export

One of three alternatives was available for this variable, each of which would have yielded different results on a calendar year basis. These were: (A) the exporter's date of application, (B) the date of application approval by the Wildlife Division, and (C) the date of intended export. I used the exporter's date of application in tabulating raw date as that most nearly correlated with the time of actual harvest and afforded the minimum inherent overlap between the close and start of successive calendar years. The date of export approval by Wildlife Division was not used because the time lag bias between harvest and export was extended by one to several weeks in all cases, principally due to mail delay in receipt and sometimes on account of irregularities in filing (form incomplete, lack of signature, etc.). Likewise, the date of intended export offered the poorest correlation with the time of actual harvest and created the greatest overlap between years. Furthermore, the date of intended export was often not specified beyond 'earliest vessel' or else altered after the application had been approved. Earlier unpublished in-house attempts at export analysis were not consistent in this approach and/or made no review of the data base and consequently were apocryphal.

As harvesting occurred throughout the year, no corrections for annual overlap in harvest records were made since all years were so effected and because the true measure of overlap was impossible to determine (i.e., an application dated 14 January contained skins that were primarily, if not exclusively, harvested during the previous year). As a result of this immeasurable bias and because such tabulations would prove needlessly unwieldy, data were not compiled to reflect a monthly analysis of exports. A priori knowledge indicated that hunter effort focused on periods of little or no moonlight and was most concentrated during the dry season when crocodiles were more accessible due to dwindled aquatic habitat (Hall, 1983). Marked variations occurred in wet/dry seasonality between harvest years and areas.

Origin of Purchases

One of the obvious shortcomings in reviewing data from export applications was that the origin of purchases could only be identified with inordinate difficulty or else not at all. At best, the origin could be attributed to a particular province and then the region (Papua or New Guinea), but not to a specific lake/lagoon or river system. When an individual application specified more than one province, and all were located within the same region, that particular consignment was accordingly tallied under the category of Mixed Papuan Provinces or Mixed New Guinean Provinces. When an export permit indicated combined skin purchases from both regions (i.e., Western and Sepik Provinces) no segregation as to origin was possible. In such an instance the only recourse was to record the shipment as 'unidentified origin.' Papua Region provinces for which 1969-1980 exports were identifiable are: Western, Gulf, and Central. Those so known from the New Guinea Region include: East and West Sepik, Madang, Morobe, Northern, East and West New Britain, and the North Solomons

(Fig. 2-1). Of necessity, the two Sepik provinces and the two New Britain provinces were each combined as one point of origin; in the first instance this was because the provinces were not separate political entities until 1975 and in both cases this was due to inconsistent identification on the export permits. However, most of the data (probably > 90%) tabled as Sepik origin stemmed from the East Sepik Province.

Species

The skins of the two crocodile species exported from PNG (*C. novaeguineae* and *C. porosus*) are readily distinguished from each other by a trained observer. New Guinea crocodiles possess about 25 transverse ventral rows between the collar and anterior vent (see Fig. 2-2), while saltwater crocodiles have 30 or more rows. Hence, traders refer to hides of the former species as 'large scale' and to the latter species as 'small scale'. Thus, the only consideration here was the implicit assumption that an exporter properly listed a consignment under the appropriate species and skin type columns when filing an application. In a few instances there was some doubt on the original applications as to the species identification of excessively large individual animals (see Tables 2-4 and 2-11).

Skin Type and Size

Skin type was classified either as belly skin (dorsal incision) or hornback (ventral incision). The methods of measurement for each type are legally defined in PNG (see Parker, 1981) and are illustrated in Figures 2-2 and 2-3. It should be noted that hornbacks prior to February 1981 (as reported herein) were formerly measured from the distal margin of the abdominal cut to the proximal edge of the third row of dorsal scutes posterior to the nuchals on each half of the skin and then summed to arrive at the actual corresponding belly skin size.

Skins and/or live crocodiles were categorized into size classes based on one inch commercial belly width increments as specified on export application forms. In general, this included size classes ranging from 4 to 20 inches belly width, except for 1972-1975 data when there was no restriction on skin size from Sepik and Madang Provinces.

Number of Skins

Tallying the numbers of skins per size class was normally a very straightforward affair with the following two exceptions.

First, live hatchlings of less than 4 inch commercial belly width were purchased during 1979 and 1980. These were included within the 4 inch size class as segregation into actual units was not possible or practical since the year class was identical.

More importantly, between 1972-1979 one or more exporters incorrectly filed their export applications by

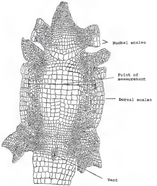

Figure 2-2. Illustration of crocodile belly skin (modified from Parker, 1981). Commercial belly skins in Papua New Guinea are measured between the distal margins of the third row of keeled dorsal scales. To be legal, a skin must not exceed 20" (51 cm) belly width and must also include at least two rows of keeled dorsal scales on either side. In 1981 a minimum size restriction of 7" (18 cm) commercial belly width was imposed.

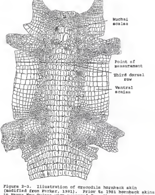

Figure 2-3. Illustration of crocodile hornback skin (modified from Parker, 1981). Prior to 1981 hornback skins in Papua New Guinea were measured from the ventral incision to the distal margin of the third row of keeled dorsal scales on each side and summed so as to exclude the dorsal row itself. Legal skins could not exceed 20" (51 cm). In 1981 the legal definition of hornbacks was changed to include only the width of the third dorsal row. Size limits were then restricted to skins between 2.5" (6 cm) and 6.5 " (17 cm).

combining the number of skins from certain size classes instead of reflecting the true size compositions. The common practice of those buyers was to purchase skins of 4/5, 6/7, and 8/9 inches on a same value per piece basis. These skins were accordingly lumped on export applications which effectively reduced the number of size classes within that range from six to three. To complicate matters further, a uniform approach in recording skins was not followed by these exporters. When reporting these data they sometimes listed them under the lower size class (e.g., 6"), whereas at other times the upper (e.g., 7") size class was used. This fact was evidently overlooked or disregarded by earlier workers when calculating size distributions of the harvest and average skin size. I circumvented this difficulty by segregating all lumped data found on export permits and adjusted them to reflect the observed summed ratios for those size classes from all exporters for that year.

Results

The trade statistics of the crocodile skin industry in PNG for the period 1969-1980 are presented in a series of tables as follows. Composite national summaries indicating the political regions and provinces of origin for each species are shown in Table 2-1 (*C. novaeguineae*) and Table 2-2 (*C. porosus*). Regional harvest summaries reflecting

Table 2-1. *Crocodylus novaeguineae* harvests in Papua New Guinea, 1969-1980.

ORIGIN	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979*	1980*	TOTALS
Papua Region													
Western Province	[illegible]	2809	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5734	[illegible]	3223	[illegible]	[illegible]	[illegible]
Gulf "	--	--	--	[illegible]	[illegible]	[illegible]	[illegible]	552	[illegible]	--	56	258	[illegible]
Central "	--	86	--	--	[illegible]	855	[illegible]	[illegible]	1886	--	86	[illegible]	[illegible]
Mixed Papuan	--	--	--	[illegible]	[illegible]	6348	[illegible]	[illegible]	4410	[illegible]	[illegible]	[illegible]	[illegible]
Region subtotal	[illegible]	3251	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
New Guinea Region													
Sepik Provinces	--	--	--	[illegible]	[illegible]	6816	[illegible]	5306	8274	[illegible]	[illegible]	9995	[illegible]
Madang "	--	--	--	59	--	6	[illegible]	1309	257	[illegible]	[illegible]	548	[illegible]
Morobe "	[illegible]	--	--	--	--	--	--	--	--	--	--	[illegible]	[illegible]
Mixed New Guinean	--	--	--	[illegible]	[illegible]	8542	[illegible]	277	[illegible]	--	[illegible]	--	[illegible]
Region subtotal	[illegible]	--	--	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Unidentified	--	--	--	--	487	[illegible]	--	894	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Totals	[illegible]	[illegible]	816	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

* Includes animals harvested alive but not exported.

Table 2-2. Crocodylus porosus harvests in Papua New Guinea, 1969-1980.

ORIGIN	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979*	1980*	TOTALS
Papua Region													
Western Province	[illegible]	65	26	1058	[illegible]	[illegible]	702	[illegible]	745	654	[illegible]	522	[illegible]
Gulf "	—	—	—	87	[illegible]	166	13	79	59	—	[illegible]	759	[illegible]
Central "	—	—	—	—	[illegible]	[illegible]	120	[illegible]	[illegible]	—	8	[illegible]	[illegible]
Mixed Papuan	—	—	—	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	1967	[illegible]	[illegible]
Region subtotal	[illegible]	88	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
New Guinea Region													
Sepik Provinces	—	—	—	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Madang "	—	—	—	8	—	[illegible]	[illegible]	—	[illegible]	—	[illegible]	40	[illegible]
Morobe "	87	59	—	—	—	—	—	—	—	—	—	[illegible]	[illegible]
Northern (Oro) "	—	—	—	—	—	[illegible]	—	[illegible]	—	—	—	26	[illegible]
Mixed New Guinean	—	—	—	[illegible]	[illegible]	[illegible]	[illegible]	4	[illegible]	[illegible]	[illegible]	—	[illegible]
Region subtotal	87	59	—	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Island Region													
New Britain	—	—	—	—	—	—	—	—	—	[illegible]	565	[illegible]	[illegible]
North Solomons	—	—	—	—	—	[illegible]	—	—	—	—	—	—	[illegible]
Unidentified	—	—	—	—	—	[illegible]	—	[illegible]	[illegible]	730	1731	1058	4699
Total	154	134	28	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

* Includes animals harvested alive but not exported

size compositions are presented in Tables 2-3 - 2-4 for C. novaeguineae and Tables 2-5 - 2-6 for C. porosus. Tables 2-3 - 2-6 exclude animals of unidentified origin listed in Tables 2-1 - 2-2. Annual national harvest summaries indicating size compositions by provincial origin appear in Tables 2-7 - 2-18 (C. novaeguineae) and Tables 2-19 - 2-30 (C. porosus). Several thousand small live crocodiles were harvested in 1979-1980 as rearing stock for large scale commercial ranches. Those animals were included in the previous tables. The size compositions of those individuals are presented separately in Tables 2-31 - 2-34. Data for the years 1969-1972 are incomplete due to missing files that I was unable to account for. Nevertheless, total harvest figures (but not species or size compositions) were available for those years (Table 2-35).

Few data were available prior to legislative attempts to regulate the crocodile skin industry. They permitted even less interpretation than the foregoing and are shown in Tables 2-36 and 2-37.

Discussion

Industry Background

Hollands (1987) identified four areas of concern that historically effected the crocodile skin industry in PNG: over-exploitation, biologically inefficient harvesting,

Table 2-3. Size compositions (in commercial belly width inches) for annual harvests of Crocodylus novaeguineae, Papua Region, Papua New Guinea. Mean size based on cohorts 4-20.

Size	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	Totals
4	201	88	10	1211	1018	100	620	1511	1218	1821	1591	189	19921
5	404	501	64	1818	2549	1134	115	1048	1080	2454	1849	1497	18132
6	640	458	99	3460	3058	2083	1301	1170	2529	2983	2908	1138	25031
7	415	218	99	2020	1818	1232	1031	2059	2039	3388	2015	1371	21181
8	348	232	98	1888	2060	2991	818	1509	1411	1488	1831	1084	15141
9	305	188	44	1099	1023	1035	817	919	881	888	1098	111	11159
10	119	148	29	1507	1101	1307	561	958	888	141	829	811	8582
11	159	91	35	1051	841	814	186	421	514	585	581	441	9308
12	111	89	21	893	819	821	285	514	418	484	551	418	9248
13	115	41	21	443	844	501	211	402	181	193	488	151	4143
14	93	95	18	488	890	421	214	381	159	338	481	109	3892
15	109	49	18	504	544	440	318	118	293	337	448	318	1815
16	118	54	21	541	511	446	285	153	308	333	451	161	3182
17	131	58	31	418	514	189	189	309	325	325	458	188	1521
18	131	58	21	489	560	331	154	194	211	214	389	291	1158
19	104	41	18	348	189	380	114	138	211	188	412	215	1421
20	125	11	18	313	198	285	81	173	269	141	518	181	1914
21	5												5
22	8												8
23	8												8
24	1												1
25	9												5
26	0												0
27	3												1
28	3												1
29	1												1
30	1												3
31	0												0
32	1												1
33	0												0
34	1												1
Totals	1893	3351	814	20281	22512	18683	1188	15882	14848	18314	16487	11144	148815
Mean	9.63	9.19	8.07	8.21	8.83	8.88	8.84	8.38	8.49	8.21	9.11	9.14	8.97

Table 2-4. Size compositions (in commercial belly width inches) for annual harvests of *Crocodylus novaeguineae*, New Guinea Region, Papua New Guinea. Mean size based on cohorts 4-20 No 1970-1971 data.

Size	1969	1972	1973	1974	1975	1976	1977	1978	1979	1980	Totals
4	0	272	1610	720	1111	505	1200	1071	2920	5041	15250
5	0	344	2043	1117	1736	714	1410	2605	2610	1011	17610
6	0	746	4747	1110	1664	874	1411	1055	1071	1142	16674
7	1	556	4085	1677	1610	741	1311	1158	1100	851	14541
8	0	166	2010	1010	916	1304	661	707	754	585	8017
9	0	115	2170	701	740	522	450	510	705	410	6381
10	1	220	1151	112	173	506	175	180	514	103	4193
11	4	104	806	101	273	101	271	147	101	109	1111
12	2	105	775	410	100	215	284	119	140	180	1803
13	0	105	701	174	161	110	101	127	241	141	1311
14	0	105	280	410	140	115	171	250	223	111	1335
15	0	170	322	506	160	141	130	210	261	144	1523
16	0	168	611	604	141	111	131	215	260	163	2410
17	0	154	561	436	133	116	145	201	287	101	2205
18	0	81	461	431	123	111	167	240	101	170	2100
19	0	10	110	207	74	101	154	240	876	161	1665
20	0	55	220	315	70	40	140	108	281	166	1421
21		10	101	171	10						178
22		21	120	120	0						277
23		22	88	81	11						217
24		20	47	11	4						117
25		8	38	54	1						101
26		11	11	10	1						36
27		8	20	17	4						68
28		1	10	23	3						46
29		9	8	17	1						37
30		6	11	30	2						50
31		1	5	8	0						15
32		1	7	7	1						16
33		0	2	4	0						6
34		1	0	1	0						4
35		1	2	1	0						4
36		0	1	1	0						1
37		0	0	0	0						0
38		0	1	1	0						1
39		3	0	1	0						1
40		0	0	0	0						0
41		0	0	0	0						0
42		0	0	0	0						0
43		0	0	0	0						0
44		0	1*	0	0						1
45		0	0	0	0						0
46		0	1*	0	0						1
Totals	9	4400	30000	12616	8094	4401	8811	11991	11870	12105	109151
Mean	10.01	9.17	9.45	9.57	7.61	8.50	7.74	7.80	7.00	6.67	8.14

* Probably misidentified *C. porosus*

Table 2-5. Size compositions (in commercial belly width inches) for annual harvests of *Crocodylus porosus*, Papua Region, Papua New Guinea. Mean size based on cohorts 4-20.

Size	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	Totals
4	19	21	0	145	420	624	344	380	424	613	189	906	3591
5	26	5	0	174	754	643	390	553	492	515	352	270	4101
6	24	11	2	289	790	811	430	530	438	514	438	352	4474
7	13	12	4	302	453	389	318	381	249	371	325	232	3249
8	16	0	5	113	401	337	209	242	170	355	219	147	2130
9	8	1	3	100	287	290	156	130	132	179	190	100	1522
10	4	1	1	79	174	294	100	92	95	135	109	93	1045
11	2	2	2	60	97	140	70	95	32	92	71	51	684
12	1	0	0	34	90	116	47	38	30	75	49	40	407
13	3	0	0	26	48	53	30	37	28	58	11	39	349
14	7	1	0	18	47	59	29	39	17	40	31	22	318
15	1	1	1	29	29	44	27	25	25	49	24	22	274
16	2	1	0	19	22	26	14	43	17	29	23	22	215
17	0	1	1	7	18	18	15	19	24	27	13	11	145
18	2	1	0	8	20	12	13	6	11	21	13	10	114
19	1	0	0	14	14	15	8	10	8	19	11	8	107
20	2	1	1	15	21	17	8	5	35	40	23	10	104
21	0												0
22	0												0
23	0												0
24	0												0
25	0												0
26	0												0
27	2												2
28	0												0
29	0												0
30	0												0
31	0												0
32	0												0
33	1												1
Totals	133	95	20	1413	3073	3569	2220	2909	2191	3035	3344	1955	22957
Mean	7.92	6.89	9.55	7.75	7.12	7.25	7.11	8.94	6.86	7.38	7.39	7.45	7.21

Table 2-6 Size compositions (in commercial belly width inches) for annual harvests of *Crocodylus porosus*, New Guinea Region (including island provinces of New Britain and North Solomons), Papua New Guinea. Mean size based on cohorts 4-20 No 1971 data

Size	1969	1970	1972	1973	1974	1975	1976	1977	1978	1979	1980	Totals
4	0	1	110	801	361	520	110	701	111	1080	1000	5987
5	0	0	110	601	168	608	601	881	111	803	528	1730
6	0	1	110	1521	807	893	183	301	813	620	830	3181
7	0	5	888	1101	866	118	188	111	188	894	333	8818
8	3	2	193	1378	181	682	318	133	183	181	283	3314
9	1	11	181	181	181	159	182	181	188	111	171	1525
10	7	11	11	881	181	168	187	111	111	101	181	1301
11	3	3	38	117	171	138	183	33	88	131	118	1333
12	1	1	13	189	183	99	83	40	84	181	183	863
13	1	1	88	181	118	18	88	72	13	88	81	880
14	1	1	80	62	88	39	81	11	11	81	72	168
15	0	3	13	60	71	13	94	52	31	31	58	383
16	1	1	33	53	37	23	51	33	53	46	37	333
17	0	1	11	18	33	20	33	31	32	33	13	331
18	0	1	13	33	31	22	30	32	30	43	33	130
19	0	1	11	33	33	30	43	31	94	31	37	131
20	0	1	11	11	88	15	21	31	81	77	11	188
21			8	18	81	8						88
22			1	18	50	8						88
23			11	13	31	3						88
24			18	18	11	8						81
25			18	11	18	8						66
26			3	1	17	3						31
27			3	13	38	1						81
28			1	1	11	1						33
29			8	1	18	8						38
30			1	1	18	1						18
31			1	3	12	3						16
32			1	1	8	1						11
33			1	3	3	3						18
34			0	0	8	0						8
35			1	1	3	0						4
36			1	1	3	0						3
37			1	3	3	0						8
38			1	8	8	1						12
39			0	0	1	0						2
40			1	4	8	1						15
41			3	3	8	0						1
42			1	2	3	0						8
43			8	1	3	3						3
44			0	8	1	0						7
45			0	1	1	0						3
46			0	3	1	0						1
47			1	0	3	1						3
48			0	0	3	0						1
49			0	0	0	0						0
50			0	0	1	0						1
Totals	11	88	2483	1333	3538	8118	8181	1818	1168	8528	8126	38166
Mean	13·88	11·88	1·11	1·11	3·31	3·33	3·54	7·17	3·52	1·39	8·11	1·66

Table 2-7. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1969. Mean size based on cohorts 4-20 Data incomplete due to missing files.

Size	Western Prov.	Papua Region	Morobe Prov	New Guinea Region	Totals
4	207	207	0	0	207
5	404	404	0	0	404
6	646	646	0	0	646
7	425	425	1	1	426
8	349	349	0	0	349
9	305	305	0	0	305
10	239	239	1	1	240
11	159	159	4	4	163
12	171	171	2	2	173
13	115	115	0	0	115
14	93	93	0	0	93
15	106	106	0	0	106
16	136	136	0	0	136
17	131	131	0	0	131
18	131	131	0	0	131
19	104	104	0	0	104
20	125	125	0	0	125
21	5	5	0	0	5
22	6	6	0	0	6
23	6	6	0	0	6
24	3	3	0	0	3
25	5	5	0	0	5
26	0	0	0	0	0
27	3	3	0	0	3
28	3	3	0	0	3
29	1	1	0	0	1
30	3	3	0	0	3
31	0	0	0	0	0
32	1	1	0	0	1
33	0	0	0	0	0
34	1	1	0	0	1
Totals	3883	3883	8	8	3891*
Mean	9.78	9.78	10.63	10.63	9.78
Percent	99.79	99.79	0.21	0.21	

* Excludes an additional 421 Western Province skins that were unidentified as to species or size.

Table 2-6. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1970. Data incomplete due to missing files.

Size	Western Prov.	Central Prov.	Papua Region	Totals
4	66	0	66	66
5	297	0	297	297
6	445	14	459	459
7	262	16	276	276
8	215	17	232	232
9	152	6	156	156
10	135	13	146	146
11	66	5	93	93
12	60	8	88	88
13	44	3	47	47
14	54	1	55	55
15	48	1	49	49
16	53	1	54	54
17	55	1	56	56
18	56	0	56	58
19	42	0	42	42
20	71	0	71	71
Totals	2165	86	2251	2251
Mean	9.10	6.93	9.10	9.10
Percent	96.16	3.82	100.00	

Table 2-9. Size composition (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1971. Data incomplete due to missing files

Size	Western Prov	Papua Region	Totals
4	10	10	94
5	94	94	94
6	99	99	99
7	69	69	69
8	66	66	66
9	44	44	44
10	29	29	29
11	25	25	25
12	21	21	21
13	21	21	21
14	16	16	16
15	18	18	18
16	21	21	21
17	17	17	17
18	23	23	23
19	16	26	16
20	25	25	25
Totals	614	614	614
Mean	9.67	9.67	9.67
Percent	100.00	100.00	

Table 2-10. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1972. Data incomplete due to missing files.

Size	Western Prov	Gulf Prov	Mixed Papuan Prov	Papua Region	Iapik Prov	Madang Prov	Mixed New Guinean Prov	New Guinea Region	Totals
1	1111	1	111	1211	103	11	194	172	1111
1	1111	88	112	1858	111	1	266	111	1111
1	1815	11	111	1111	111	11	601	141	1318
7	1111	11	111	1126	118	1	311	118	1101
1	1111	11	311	1168	11	11	111	111	1111
1	1111	11	111	1150	11	8	142	111	8194
10	1171	11	111	1507	88	1	151	828	1717
11	111	11	118	1011	11	1	118	194	1111
11	181	11	11	162	48	1	141	111	1181
11	111	11	78	163	56	1	111	161	111
11	601	18	15	860	34	1	111	160	111
11	511	11	62	111	77	1	99	157	718
11	111	12	11	111	48	1	158	111	711
11	881	1	17	111	88	1	88	118	118
18	811	11	11	881	11	1	11	11	171
11	111	1	23	181	23	1	11	11	111
11	178	1	11	111	18	8	21	11	148
11					13	1	17	11	11
22					12	1	1	11	11
13					11	8	11	82	11
11					11	1	1	11	11
11					1	1	1	1	1
11					1	1	10	11	11
27					3	1	5	0	1
11					1	1	1	1	1
81					0	8	8	8	8
11					1	1	1	1	1
81					1	0	1	1	1
11					1	1	1	1	1
11					1	1	1	1	8
11					1	1	1	1	8
25					1	1	1	1	1
11					1	1	1	1	1
11					1	1	1	1	1
18					1	8	8	1	8
11					1	1	1	1	1
Totals	17117	171	2611	16807	1411	11	1891	1108	14607
Mean	1 11	1 11	8 11	8 11	1 22	1 11	1 66	1 11	1 11
Percent	66 96	1 11	10 60	11 11	3 11	1 11	11 11	11 11	

Table 2-11. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1973

Size	Western Prov	Gulf Prov	Central Prov	mixed Papuan Prov	Papua Region	Sepik Prov	mixed New Guinea Prov	New Guinea Region	unidentified origin	Totals
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
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[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
[illegible]						[illegible]	[illegible]	[illegible]		[illegible]
Totals	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Mean	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Percent	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	

* Probably misidentified *C. porosus*

Table 2-12. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1974.

Size	Western Prov	Gulf Prov	Central Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	Mixed New Guinean Prov	New Guinea Region	Unidentified Origin	Totals
1	111	15	0	111	108	410	0	138	118	0	1115
0	115	15	0	511	1111	511	5	115	1159	5	1699
0	1150	50	64	515	1103	1011	1	650	1160	15	1690
5	2166	15	04	911	1111	1111	5	441	1115	10	5127
0	1111	60	51	110	1101	411	1	301	1030	0	1510
9	1331	11	15	311	1115	111	1	295	161	5	1151
10	011	25	18	411	1111	111	0	179	515	5	1914
11	115	21	10	111	131	111	1	103	507	5	1191
15	130	15	11	101	111	111	0	311	130	0	1081
21	111	0	15	110	103	111	1	131	154	5	815
31	111	10	11	115	421	015	0	111	130	5	141
15	111	1	13	110	115	114	1	101	506	1	950
30	111	1	5	310	110	111	1	311	504	1	011
31	110	11	15	11	101	111	1	357	111	5	011
31	231	0	15	13	175	111	1	111	411	0	568
35	110	1	30	15	100	104	1	111	151	1	572
10	115	1	1	15	105	115	0	101	111	1	511
11						15	0	11	151		111
15						10	0	11	111		111
11						90	0	10	01		11
11						15	0	11	91		11
15						14	0	10	11		54
10						25	0	12	11		11
11						10	0	1	21		21
11						15	0	1	11		11
21						11	5	1	11		11
11						11	0	1	11		11
11						5	5	1	1		1
11						1	0	1	1		1
11						4	0	1	1		1
11						1	5	1	1		1
31						1	0	1	1		1
11						1	0	1	1		1
11						1	0	1	5		1
11						1	0	1	1		1
11						1	5	1	1		1
Totals	32111	165	158	5801	18111	8115	1	1111	11806	202	32154
Mean	0.12	0.21	0 51	1 15	0 00	25 11	12 51	20.11	20 18	0 97	0 42
Percent	35 15	1 11	1 14	11 18	30 18	11 11	0 01	31 11	11 12	0 11	

Table 2-13. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1975.

Size	Western Prov	Gulf Prov	Central Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	Mixed New Guinean Prov	New Guinea Region	Totals
4	112	0	166	126	626	1102	1	14	1123	1760
5	118	0	266	261	116	1666	11	10	1118	3591
6	686	4	122	280	1101	1611	19	32	1834	1165
7	614	0	168	219	1011	1618	24	10	1630	3661
8	468	50	152	166	828	882	21	11	616	1144
9	147	81	100	186	611	121	11	11	149	1166
10	184	41	86	124	661	115	21	11	313	614
11	210	40	46	60	166	261	16	6	273	839
12	161	40	43	46	165	171	11	6	160	405
13	110	16	10	16	111	141	14	4	161	112
14	126	12	15	42	214	121	12	5	140	354
15	116	16	24	46	210	136	16	5	160	310
16	126	14	14	12	206	118	22	8	141	346
17	142	13	24	16	166	108	21	12	131	320
18	111	2	16	16	154	96	11	14	121	261
19	86	3	11	11	114	56	15	1	14	180
20	64	5	10	4	83	61	19	0	16	162
21						16	0	3	16	16
22						1	0	1	8	8
23						8	0	1	11	11
24						3	0	1	4	4
25						2	0	1	1	3
26						2	0	0	8	2
27						1	0	1	4	4
28						1	0	0	3	1
29						1	0	0	1	1
30						2	0	0	2	2
31						0	0	0	0	0
32						1	0	0	1	1
Totals	4164	311	1660	1521	1186	6411	184	186	9984	11660
Mean	6 34	11 10	1 83	8 23	8 04	1 49	12 05	11 02	1 10	8 20
Percent	24 18	1 81	5 76	5 08	44 01	53 38	1 71	1 01	66 08	

Table 2-14. Size compositions (in commercial belly width inches) for national harvest of Crocodylus novaeguineae, Papua New Guinea, 1976.

Size	Western Prov	Gulf Prov	Central Prov	mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	mixed New Guinean Prov	New Guinea Region	unidentified origin	Totals
4	2002	2	423	188	1527	585	0	0	585	25	2022
5	817	20	824	378	1515	718	0	4	721	65	2711
6	1102	11	888	181	1211	568	0	11	871	101	4451
7	2162	8	427	157	2025	681	46	27	742	11	2887
8	825	14	442	222	1509	146	788	21	1284	86	1878
9	185	18	240	68	515	113	178	29	522	58	2488
10	499	48	238	83	858	185	172	20	184	51	1518
11	416	18	135	38	621	188	88	22	181	38	567
12	128	18	123	15	318	146	41	22	215	65	181
13	145	11	86	27	481	118	8	8	218	81	311
14	140	17	51	21	182	107	18	14	115	52	571
15	220	17	76	15	328	121	0	22	211	22	158
16	225	15	84	23	351	55	0	20	227	25	505
17	102	14	66	21	185	180	0	14	224	24	111
18	105	14	57	20	296	198	0	7	229	11	121
19	175	11	17	7	120	51	0	10	202	6	222
20	127	2	14	7	172	15	0	5	16	6	222
Totals	9704	252	4614	1282	15882	5284	1250	227	6691	681	11178
Mean	8.40	12.18	7.16	7.51	8.18	8.11	8.11	12.10	8.58	5.87	8.47
Percent	42.52	2.22	20.86	5.86	67.54	22.27	3.25	2.01	28.82	2.11	

Table 2-15. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1977.

Size	Western Prov	Gulf Prov	Central Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	Mixed New Guinean Prov	New Guinea Region	Unidentified origin	Totals
4	788	0	801	334	1888	1108	0	338	1298	180	1798
5	888	0	819	481	1538	8108	0	388	1878	878	4810
6	1981	1	883	458	8829	1108	48	398	1813	881	4171
7	1881	0	898	338	1839	988	0	288	1111	879	3818
8	881	8	808	298	1817	518	81	89	648	288	1198
9	888	8	178	188	888	888	3	48	499	188	1918
10	818	81	188	318	888	319	18	48	878	811	3368
11	888	88	38	98	518	138	8	18	378	188	981
12	291	88	109	81	478	231	3	18	388	178	808
13	318	16	71	53	381	381	7	11	191	161	718
14	317	14	67	52	310	183	8	81	171	154	885
15	388	38	81	33	388	156	8	34	178	198	886
16	177	7	68	52	300	247	8	31	178	118	988
17	188	33	99	88	389	181	8	8	188	100	888
18	141	33	38	39	317	188	8	38	387	81	899
19	114	7	38	35	213	130	8	88	388	87	814
20	188	5	38	41	289	131	1	8	380	81	888
Totals	8118	188	8118	1918	18888	8278	187	1182	8813	2818	18971
Mean	8.71	11.21	8.08	8.08	8.49	8.78	10.81	7.18	7.78	10.07	8.88
Percent	81.88	0.67	11.88	9.47	81.87	31.14	0.59	4.49	36.10	10.88	

Table 2-16. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1978.

Size	Western Prov.	Mixed Papuan Prov.	Papua Region	Sepik Prov.	Morobe Prov.	New Guinea Region	Unidentified origin	Totals
4	233	1590	1823	1763	108	1871	5	3699
5	387	2067	2454	2603	92	2695	3	5152
6	592	2389	2981	1853	106	1959	0	4940
7	512	1794	2306	1280	78	1358	4	3666
8	354	1142	1496	729	58	787	236	2519
9	239	729	968	497	31	528	212	1708
10	156	587	743	330	30	360	247	1350
11	114	451	565	227	20	247	242	1054
12	101	393	494	224	15	239	275	1008
13	78	274	352	207	20	227	241	820
14	70	266	336	215	35	250	210	796
15	56	281	337	218	21	239	228	804
16	71	260	331	249	26	275	212	818
17	74	251	325	276	5	281	185	791
18	50	224	274	233	13	246	173	693
19	49	139	188	234	6	240	117	545
20	86	255	341	184	6	190	90	621
Totals	3222	13092	16314	11322	670	11992	2680	30986
Mean	8.63	8.14	8.23	7.85	8.29	7.88	13.23	8.53
Percent	10.40	42.25	52.65	36.54	2.16	38.70	8.65	

Table 2-17. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1979 (includes live crocodile purchases - see Table 2-31)

Size	Western Prov	Gulf Prov	Central Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	Mixed New Guinean Prov	New Guinea Region	Unidentified origin	Totals
4	406	21	25	841	1562	2212	188	338	3803	338	4631
5	811	38	3	1288	2644	1534	328	884	3828	788	3235
6	383	23	7	1878	3358	1328	178	318	1831	2217	5833
7	336	17	29	1543	3036	330	143	508	1280	808	4204
8	257	7	4	1283	1627	288	83	318	756	1042	3335
9	132	6	5	883	1088	342	23	218	305	792	2594
10	137	1	2	888	829	355	21	123	514	643	2037
11	109	6	4	378	883	378	32	103	382	485	1725
12	88	6	2	367	553	318	28	123	348	432	2317
13	73	5	3	312	363	148	14	63	342	283	1102
14	83	6	5	314	263	133	14	86	227	323	2023
15	73	9	3	272	348	162	18	33	361	283	1096
16	63	9	2	288	251	166	21	83	369	231	1112
17	63	8	8	278	330	232	18	303	393	252	1103
18	59	8	1	228	388	237	18	37	202	308	1053
19	30	8	0	233	837	289	8	24	276	277	868
20	71	6	3	363	538	183	14	82	231	382	1133
Totals	2382	88	88	22233	26488	6582	1013	2974	12878	8221	38312
Mean	3.12	8.83	8.18	8.46	8.32	7.80	3.22	3.22	7.88	28.27	8.88
Percent	8.58	4.23	3.22	32.28	21.83	21.77	3.83	18.22	33.88	23.69	

Table 2-18. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus novaeguineae*, Papua New Guinea, 1980 (includes live crocodile purchases - see Table 2-12)

Size	Western Prov.	Gulf Prov.	Central Prov.	Mixed Papuan Prov.	Papua Region	Sepik Prov	Madang Prov.	Morobe Prov.	New Guinea Region	unidentified origin	Totals
1	101	22	202	105	780	4001	135	211	1011	108	0210
5	175	10	405	100	1401	1101	201	117	1021	100	4200
8	121	57	431	114	2720	001	79	210	1342	2013	4781
1	101	47	201	122	2171	710	80	297	001	2110	1010
1	102	21	280	125	1090	421	26	131	505	2112	2020
9	100	21	150	202	772	210	22	11	410	1010	1211
20	202	8	218	120	072	250	20	01	162	111	1010
21	102	2	02	144	442	131	12	15	180	507	1101
21	150	0	201	217	420	120	0	21	186	514	2120
11	129	2	80	217	157	100	0	20	141	151	002
11	104	2	00	210	100	07	0	25	111	451	004
11	112	7	75	218	110	00	0	10	144	115	020
26	140	8	02	211	102	125	0	28	161	110	000
27	100	2	78	211	100	122	22	21	262	101	040
18	07	12	80	227	101	112	20	40	178	201	869
20	01	2	55	210	175	118	10	42	101	271	009
10	85	8	81	250	161	127	22	10	166	401	962
Totals	1041	257	1700	2201	11286	9990	540	1618	12205	22037	15370
Mean	8.00	8 10	6.02	10 01	8 10	8 10	7 61	6 02	6.01	10 22	8 70
Percent	11 07	0 72	7 00	0 06	22 56	20 20	2 55	1 02	24 11	21.80	

Table 2-19. Size compositions (in commercial belly width inches) for national harvest of Crocodylus porosus, Papua New Guinea, 1969. Mean size based on cohorts 4-20. Data incomplete due to missing files.

Size	Western Prov.	Papua Region	Morobe Prov.	New Guinea Region	Totals
4	18	18	0	0	18
5	26	26	0	0	26
6	24	24	0	0	24
7	13	13	0	0	13
8	16	16	5	5	21
9	8	8	1	1	9
10	4	4	7	7	11
11	2	2	2	2	4
12	1	1	3	3	4
13	3	3	1	1	4
14	7	7	1	1	8
15	1	1	0	0	1
16	2	2	1	1	3
17	0	0	0	0	0
18	2	2	0	0	2
19	1	1	0	0	1
20	2	2	0	0	2
21	0	0	0	0	0
22	0	0	0	0	0
23	0	0	0	0	0
24	0	0	0	0	0
25	0	0	0	0	0
26	0	0	0	0	0
27	2	2	0	0	2
28	0	0	0	0	0
28	0	0	0	0	0
30	0	0	0	0	0
31	0	0	0	0	0
32	0	0	0	0	0
33	1	1	0	0	1
Totals	133	133	21	21	154
Mean	8.10	8.10	10.48	10.48	8.42
Percent	86.36	86.36	13.64	13.64	

Table 2-20. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus porosus*, Papua New Guinea, 1970. Data incomplete due to missing files.

Size	Western Prov	Papua Region	Morobe Prov.	New Guinea Region	Totals
4	21	21	1	1	22
5	5	5	5	5	5
6	11	11	1	1	12
7	12	12	5	5	17
8	6	6	2	2	8
9	1	1	12	12	13
10	1	1	11	11	12
11	2	2	6	6	8
12	0	0	3	3	3
13	0	0	3	3	3
14	1	1	3	3	4
15	1	1	2	2	3
16	1	1	1	1	2
17	1	1	1	1	2
18	1	1	2	2	3
19	0	0	3	3	3
20	1	1	3	3	4
Totals	65	65	59	59	124
Mean	6.99	6.99	11.49	11.49	9.09
Percent	52.42	52.42	47.58	47.58	

Table 2-21. Size composition (in commercial belly width inches) for national harvest of *Crocodylus porosus*, Papua New Guinea, 1971. Data incomplete due to missing files.

Size	Western Prov.	Papua Region	Totals
4	0	0	0
5	0	0	0
6	2	2	2
7	4	4	4
8	5	5	5
9	3	3	3
10	1	1	1
11	2	2	2
12	0	0	0
13	0	0	0
14	0	0	0
15	1	1	1
16	0	0	0
17	1	1	1
18	0	0	0
19	0	0	0
20	1	1	1
Totals	20	20	20
Mean	9.55	9.55	9.55
Percent	100.00	100.00	

Table 2-22. Size compositions (in commercial belly width inches) for national harvest of Crocodylus porosus, Papua New Guinea, 1972. Data incomplete due to missing files.

Size	Western Prov	Gulf Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	Mixed New Guinean Prov	New Guinea Region	Totals
4	318	2	15	383	38	0	154	138	338
5	144	8	26	124	28	0	188	214	388
6	332	8	31	389	68	3	833	538	888
7	383	3	88	393	313	0	883	688	838
8	68	3	88	112	38	3	364	333	338
9	58	3	88	300	24	0	188	183	382
10	83	3	28	33	13	1	79	83	338
11	36	3	33	80	25	0	79	38	364
12	38	3	8	38	38	3	88	83	338
13	13	0	33	38	3	0	83	88	78
14	11	3	8	18	6	0	38	48	58
15	23	0	3	28	0	0	27	32	88
16	22	0	0	18	0	0	39	26	83
17	8	0	3	3	3	0	8	33	38
18	5	0	3	0	0	0	7	12	20
19	8	0	0	14	3	0	13	35	38
20	28	0	3	38	3	0	3	22	38
21					3	3	8	8	8
22					3	0	3	3	3
23					3	0	8	13	13
24					3	0	7	10	10
25					6	0	8	10	10
26					2	0	3	3	3
27					3	0	1	3	3
28					0	0	3	3	3
29					3	0	3	8	8
30					1	1	1	1	3
31					0	0	3	3	3
32					3	3	3	3	3
33					1	0	3	3	3
34					0	0	0	0	0
35					3	0	0	1	1
36					3	0	0	3	3
37					0	0	3	2	2
38					0	0	3	3	3
39					0	0	0	0	0
40					0	0	3	3	3
41					0	0	2	2	2
42					1	0	0	1	3
43					2	0	2	0	0
44					0	0	0	2	0
45					0	0	0	0	0
46					0	0	0	0	0
47					0	0	3	3	3
Totals	1838	27	328	1413	838	3	2038	3882	3237
Mean	3.83	7.83	8.67	2.32	8.38	13.11	8.38	8.38	8.33
Percent	33.38	8.40	8.47	38.33	23.33	8.28	82.32	83.73	

Table 2-23. Size compositions (in commercial belly width inches) for national harvest of Crocodylus porosus, Papua New Guinea, 1973.

Size	Western Prov.	Gulf Prov.	Central Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Mixed New Guinean Prov	New Guinea Region	Totals
1	111	1	18	881	111	111	111	111	119
5	111	1	13	528	164	811	111	111	1681
8	111	1	84	581	111	881	571	1118	1111
7	111	1	11	111	111	111	111	1863	1116
1	125	8	67	111	111	111	897	1578	1114
1	85	3	71	111	111	111	881	111	1868
11	11	1	38	89	111	111	136	481	165
11	11	1	85	86	87	176	165	331	111
12	8	1	23	88	80	129	64	189	118
13	11	1	19	11	61	68	11	181	111
14	22	8	11	11	17	52	18	48	181
11	11	1	8	11	29	11	18	61	88
11	1	1	8	18	11	11	11	11	11
87	1	1	1	7	11	11	1	11	54
11	8	1	11	1	10	11	86	81	54
11	1	0	1	6	11	11	6	18	81
60	1	1	1	1	81	11	1	11	11
11						18	11	11	11
22						11	1	11	11
11						11	2	18	11
11						11	1	28	21
11						11	1	11	11
81						5	1	1	1
81						1	1	11	11
11						1	1	7	1
23						1	1	1	8
11						1	1	1	1
11						1	1	1	1
11						8	1	1	1
11						1	1	1	4
34						1	6	1	1
35						1	8	1	1
11						1	1	3	1
11						8	1	8	1
11						1	8	1	6
11						1	1	8	1
11						3	1	8	1
11						1	1	1	1
11						1	8	1	1
11						1	6	1	1
11						1	1	1	1
11						1	1	3	1
11						1	1	1	1
Totals	1811	1	466	1111	1071	1100	4781	7111	11111
Mean	1 11	1-11	8 80	1 71	1 12	1 11	8 11	1 11	1 11
Percent	10 60	1 11	1 11	11 79	11 11	41 11	11 11	66 11	

Table 2-24. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus porosus*, Papua New Guinea, 1974.

Size	Western Prov	Gulf Prov	Central Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	Northern Prov	North Solomons Prov	Mixed New Guinea Prov	New Guinea Region	Unidentified origin	Totals
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table 2-25. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus porosus*, Papua New Guinea, 1975.

Size	Western Prov	Gulf Prov	Central Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	Mixed New Guinea Prov	New Guinea Region	Totals
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]						[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Totals	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Mean	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Percent	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	

Table 2-26. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus porosus*, Papua New Guinea, 1976.

size	Western Prov.	Gulf Prov.	Central Prov.	mixed Papuan Prov	Papua Region	Sepik Prov.	Northern Prov	mixed New Guinean Prov	New Guinea Region	unidentified origin	Totals
4	201	1	94	88	333	328	0	0	336	72	707
5	203	12	202	143	503	831	1	0	542	101	1108
6	132	25	340	81	830	108	0	1	380	92	1020
7	130	18	144	81	381	138	18	0	248	78	702
8	111	18	82	38	252	207	0	1	214	105	561
9	33	0	38	17	130	133	4	0	132	81	373
10	38	3	37	12	83	138	3	0	130	82	313
11	23	3	33	7	88	83	5	0	100	74	235
12	13	2	20	2	38	83	3	0	38	33	170
13	13	3	12	0	37	33	1	0	88	54	171
14	12	2	12	13	38	53	1	1	61	38	138
15	5	5	12	2	25	54	0	0	83	28	103
16	12	7	14	0	33	81	0	0	51	28	124
17	10	2	0	2	10	33	3	0	38	28	88
18	3	0	3	0	8	28	2	0	30	11	57
19	5	2	2	1	10	33	0	0	33	10	72
20	0	0	0	0	0	18	0	1	22	4	21
Totals	1934	88	887	818	2888	2488	38	3	3747	901	6287
Mean	6.02	6.78	7.05	6.59	6.98	7.07	11.21	12.03	8.04	9.21	7.78
Percent	18.82	1.08	15.38	8.38	31.78	33.07	0.77	0.08	33.88	13.38	

Table 2-27. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus porosus*, Papua New Guinea, 1977.

Size	Western Prov	Gulf Prov	Central Prov	mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	mixed New Guinean Prov	New Guinea Region	unidentified origin	Totals
4	152	0	137	144	424	531	0	56	557	29	1929
5	139	0	172	172	402	554	9	111	985	74	1501
6	135	1	199	322	438	449	55	42	547	87	1072
7	80	1	55	72	149	159	19	41	117	62	629
8	52	1	91	51	178	127	55	0	108	50	429
9	42	1	49	41	111	111	41	20	101	99	179
10	35	10	18	10	55	85	15	15	125	115	185
11	15	5	6	9	11	71	5	5	81	94	189
12	39	4	5	5	35	75	5	8	99	85	204
13	32	4	9	4	26	56	0	6	72	41	159
14	4	1	5	4	17	51	1	1	51	51	135
15	32	4	4	5	25	48	4	2	52	52	135
16	7	5	5	1	17	19	1	2	38	64	119
17	7	5	0	2	14	11	4	0	17	39	50
18	4	1	2	1	11	29	2	1	32	27	79
19	4	0	2	0	6	17	5	0	17	27	78
20	10	9	9	9	35	45	1	0	47	13	95
Totals	745	58	785	881	2151	2911	116	211	2459	999	8618
Mean	7.42	13.01	6.48	5.25	5.55	7.25	8.56	6.55	7.27	10.77	7.57
Percent	11.21	0.75	10.85	9.99	31.95	41.89	1.25	5.01	52.27	15.85	

Table 2-28. Size compositions (in commercial belly width inches) for national harvest of Crocodylus porosus, Papua New Guinea, 1978.

Size	Western Prov	mixed Papuan Prov	Papua Region	Sepik Prov	New Britain Prov	mixed New Guinean Prov	New Guinea Region	unidentified origin	Totals
4	101	513	913	783	21	3	737	8	1348
5	104	311	515	883	39	38	353	3	1373
6	158	303	514	350	29	38	338	3	953
7	87	304	333	188	35	33	338	7	738
8	84	191	239	318	34	33	183	38	475
9	33	148	179	98	34	33	158	54	393
10	33	103	135	78	38	13	131	319	378
11	17	75	92	35	24	37	88	158	278
12	27	58	75	32	38	33	84	98	355
13	13	47	58	44	35	17	78	74	288
14	10	32	40	30	34	18	72	88	308
15	27	33	40	33	22	8	83	41	153
16	6	20	30	28	12	12	52	33	138
17	8	39	27	32	3	8	43	27	88
18	7	33	23	27	10	3	48	38	93
19	8	13	30	40	33	3	84	28	83
20	19	31	39	37	13	12	81	18	119
Totals	854	2381	3035	3852	382	330	2383	738	7357
Mean	3.93	3 13	7 20	3 04	10 29	9 81	7.53	12 58	7 95
Percent	9 13	33 37	33 31	37 05	5 33	3.09	33.27	18 93	

Table 2-29. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus porosus*, Papua New Guinea, 1979 (includes live crocodile purchases - see Table 2-33).

Size	Western Prov	Gulf Prov	Central Prov	mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	New Britain Prov	mixed New Guinean Prov	New Guinea Region	unidentified origin	Totals
4	8	29	7	744	857	587	15	18	64	1085	779	1749
5	8	32	7	775	858	654	22	67	135	556	207	1447
6	48	15	7	850	670	758	17	58	151	880	778	1758
7	86	17	0	788	875	749	8	51	156	484	788	508
8	77	8	0	185	718	158	5	71	117	861	748	708
9	71	7	0	187	168	85	5	55	78	811	788	588
10	18	2	0	58	108	77	5	58	78	817	768	668
11	5	7	0	65	81	54	5	38	87	187	705	308
12	8	0	0	38	46	69	5	35	77	107	58	245
13	2	0	0	78	81	86	7	75	88	55	78	185
14	4	0	0	77	81	15	7	78	18	68	78	187
15	8	0	0	77	76	15	7	17	28	52	66	187
16	1	0	0	77	88	15	7	5	18	64	78	57
17	0	0	0	77	18	71	1	71	18	87	78	55
18	0	0	0	17	17	17	1	13	17	67	87	85
19	0	0	0	11	11	28	0	8	18	67	78	87
20	0	0	0	77	88	66	4	18	17	77	85	185
Totals	187	102	8	1909	7866	8856	706	565	598	4525	1881	8608
Mean	8.62	5.50	5.00	7.29	7.76	6.75	8.08	8.57	8.47	8.78	8.85	7.48
Percent	7.18	1.15	0.06	77.78	88.88	88.77	1.88	6.57	11.68	58.67	21.89	

Table 2-30. Size compositions (in commercial belly width inches) for national harvest of *Crocodylus porosus*, Papua New Guinea, 1980 (includes live crocodile purchases - see Table 2-34).

Size	Western Prov	Gulf Prov	Central Prov	Mixed Papuan Prov	Papua Region	Sepik Prov	Madang Prov	Morobe Prov	New Britain Prov	New Guinea Region	Unidentified Origin	Totals
4	39	34	54	96	164	1515	11	33	11	1636	193	3039
5	83	62	99	15	278	391	16	13	27	505	225	1099
6	136	35	10	16	351	311	8	166	93	436	211	1113
7	88	39	48	35	232	114	3	11	53	135	204	781
8	36	15	15	33	141	101	5	48	13	116	307	580
9	10	9	15	38	166	77	1	51	84	201	111	318
10	16	8	36	39	83	57	1	13	66	161	151	306
11	14	1	33	13	91	31	8	11	56	116	136	276
12	10	1	11	15	48	39	1	16	15	105	53	131
13	7	1	16	11	16	10	0	18	17	81	11	199
14	5	1	8	10	22	15	6	11	48	11	73	168
15	11	1	3	1	11	15	0	11	11	90	96	136
16	11	6	8	5	22	10	1	1	15	41	58	129
17	1	0	8	3	11	10	0	1	19	36	29	10
18	0	6	3	8	16	11	9	1	20	44	11	87
19	5	0	0	3	8	13	0	0	16	41	22	11
20	5	6	0	13	16	39	0	1	41	11	55	144
Totals	522	158	411	361	1855	2935	42	531	311	2225	2058	3818
Mean	1.33	8.10	1.75	1.36	1.48	9.33	6.30	8.11	11.11	6.81	3.91	3.66
Percent	6.58	3.16	9.15	5.33	10.85	16.91	6.56	6.11	8.02	51.23	15.83	

Table 2-31. Live *Crocodylus novaeguineae* purchases included in 1979 national harvest summary (Table 2-17). Size expressed in commercial belly width inches.

Size	Western Prov.	Gulf Prov.	Central Prov.	Papua Region	Sepik Prov.	New Guinea Region	Totals
4	608	11	15	832	1491	1491	2123
5	511	29	8	548	348	348	896
6	318	25	3	348	143	143	489
7	212	17	7	236	52	52	288
8	84	7	0	71	19	19	90
9	12	6	2	20	5	5	25
10	5	1	0	6	2	2	8
11	2	0	2	4	2	2	6
12	1	0	2	3	2	2	5
13	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0
20	0	0	1	1	0	0	1
Totals	1731	96	40	1867	2064	2064	3931

Table 2-32. Live *Crocodylus novaeguineae* purchases included in 1980 national harvest summary (Table 2-18). Size expressed in commercial belly width inches.

Size	Western Prov.	Gulf Prov.	Central Prov.	Papua Region	Sepik Prov.	New Guinea Region	Totals
4	307	12	44	363	4046	4046	4409
5	768	27	19	814	662	662	1476
6	683	26	5	714	263	263	977
7	373	23	6	402	99	99	501
8	124	8	4	136	45	45	181
9	58	4	4	66	13	13	79
10	23	0	4	27	4	4	31
11	6	1	1	8	1	1	9
12	1	0	2	3	0	0	3
13	0	0	2	2	0	0	2
14	0	0	0	0	0	0	0
15	0	0	1	1	0	0	1
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0
Totals	2343	101	92	2536	5133	5133	7669

Table 2-33. Live *Crocodylus porosus* purchases included in 1979 national harvest summary (Table 2-29). Size expressed in commercial belly width inches.

Size	Western Prov.	Gulf Prov	Central Prov	Papua Region	Sepik Prov.	New Guinea Region	Totals
4	7	29	0	36	648	648	684
5	3	32	2	37	107	107	144
6	0	18	2	20	65	65	85
7	0	12	2	14	17	17	31
8	0	8	0	8	12	12	20
9	0	2	0	2	4	4	6
10	0	0	0	0	2	2	2
11	0	1	0	1	1	1	2
12	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0
Totals	10	102	6	118	856	856	974

Table 2-34. Live *Crocodylus porosus* purchases included in 1980 national harvest summary (Table 2-30). Size expressed in commercial belly width inches.

Size	Western Prov.	Gulf Prov.	Central Prov.	Papua Region	Sepik Prov.	New Guinea Region	Totals
4	49	44	3	96	1379	1379	1475
5	77	60	0	137	186	186	323
6	31	73	0	104	87	87	191
7	12	33	1	46	55	55	101
8	1	5	0	6	30	30	36
9	0	4	0	4	5	5	9
10	0	3	0	3	2	2	5
11	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0
13	0	1	0	1	0	0	1
14	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0
Totals	170	223	4	397	1744	1744	2141

Table 2-35. Crocodile exports from Papua New Guinea, 1969-1972. Source: Puffet (unpubl. - Wildlife Division file 14-9-19 part 1). Species and size compositions unknown.

Area	1969	1970	1971	1972
Papua	12056	8002	8204	32532
New Guinea	14463	21093	12257	11440
New Britain	575	773	674	1213
Totals	27094	29868	21135	45185

Table 2-36 Crocodile (Crocodylus novaeguineae and C. porosus) skin purchases from Papua New Guinea, 1959-1968, by Booth and Company. Species composition unknown except for Milne Bay and Manus Provinces (all C. porosus) and 1968 calendar year (20% C. porosus).

ORIGIN	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	TOTALS
Papua Region											
Western Province	3476	1098	3421	9909	14831	9798	8818	7781	1172	21	51400
Gulf "	—	916	76	70	1050	110	87	—	—	—	1319
Central "	—	—	—	84	166	2301	91	—	—	—	1823
Milne Bay "	85	291	266	388	388	398	199	174	115	208	2316
Mixed Papuan	179	508	1349	2000	2688	1261	8311	8920	3036	3238	24865
Region subtotal	3742	4250	6164	7521	10068	18017	9192	8893	9032	3869	84993
New Guinea Region											
Sepik Provinces	1177	2892	2189	1445	1359	3627	2619	6620	2008	1669	27283
Northern Province	—	—	—	—	—	18	0	19	—	—	37
Manus Province	—	—	—	92	160	17	—	—	—	18	309
Region subtotal	2177	2892	2189	9698	1421	3044	2419	4689	1000	1803	27992
Totals	5019	4751	10295	9986	20769	19881	11611	14503	7098	5346	111942

Table 2-37. Papua New Guinea crocodile (*Crocodylus novaeguineae* and *C. porosus*) harvest statistics for the July-June periods from 1960 to 1969. Sample harvests are from the files of a single exporter (Booth and Company). Mean skin sizes are based on those samples. Estimated harvests for these periods are from Hollands (1987). Species composition of harvests is unknown.

Years	1960-61	1961-62	1962-63	1963-64	1964-65	1965-66	1966-67	1967-68	1968-69	Totals
Sample harvest	4486	6878	11566	22927	10300	15391	11289	5954	2643	98108
Mean size (inches)	11.81	12.79	12.11	11.98	11.82	11.45	11.09	12.10	11.38	11.81
Estimated harvest	10410	59000	74300	79300	88260	79000	53100	36800	20560	499410

economics, and poor international marketing. A brief synopsis follows.

Prior to the imposition of legislative controls, the preferred trade in PNG was for large adult crocodiles (especially *C. porosus*) which rapidly diminished the wild breeding stock. Consequently, hunters increasingly relied on the cropping of small animals with little economic value. This resulted in drastically larger harvests during the 1960's and altered population compositions to the extent that conservationists feared the harvest could no longer be sustained and that PNG crocodiles were imperiled with extinction (Neill, 1971). Fortunately, those views proved to be rather alarmist. Nevertheless, they did help inspire early management actions.

Concurrently, villager hunters derived marginal returns on the true value of their resource from expatriate traders. Additionally, national revenues were suppressed since the bulk of exports were marketed through Singapore middlemen, rather than through direct contact with European and Japanese tanneries. A further combination of poor skinning and preservation techniques, plus the inclusion of less valuable hornback hides, helped to depress the potential economic return. Trade in hornback hides (principally from the Sepik provinces) was very popular with the Japanese market in the mid-1970's (it comprised nearly half of the 1973 total exports), but diminished to almost nil by the end of the decade. A colorful perspective on the life and times of a crocodile trader during this period is provided by Pinney (1976).

During 1976 a marketing service for crocodile skins was established by the national government to help ensure fair market competition with private sector interests. This action, along with extension activities aimed at improving the quality of hides through better skinning and preservation, greatly enhanced revenue return among village resource owners and helped foster receptivity toward conservation and management policies. These latter aspects were further strengthened through a policy shift in the late 1970's to replace the hunting for skins of very small crocodiles by the live harvest of those animals for rearing to commercial size. Under this policy hunters received far higher prices for a live animal than for a comparable size skin and thus could earn a greater income from harvesting fewer crocodiles. I refer readers to Hollands (1987) for a more thorough authoritative treatment on this subject.

Harvest Figures

The otherwise excellent review paper by Hollands (1987) on the management of Papua New Guinea crocodiles is marred by inaccurate harvest figures (p. 76) for years in which data could be substantiated, rather than speculated. Table 2-38 indicates these data along with the comparative

Table 2-38. Comparative harvest figures for Crocodylus novaeguineae and C. porosus from Papua New Guinea. Corrected values are reported on the right.

Source	Hollands (1987)				This study		
Year	C. n.	C. p.	Totals	Year	C. n.	C. p.	Totals
1968-1969	--	--	26500	--	--	--	--
1969-1970	--	--	34146	1969	--	--	27084
1970-1971	--	--	24429	1970	--	--	29868
1971-1972	--	--	23367	1971	--	--	22135
1972-1973	--	--	25937	1972	--	--	45185
1973	51439	11453	62892	1973	51439	11453	62892
1974	62948	7272	70220	1974	31474	7272	36746
1975	17690	6974	24664	1975	17690	6474	24164
1976	23379	6257	29636	1976	23379	6257	29636
1977	26571	6616	33189	1977	26571	6618	33189
1978	30886	7157	38043	1978	30986	7157	38143
1979	35474*	7626*	43100*	1979	35482*	7626*	43108*
1980	27709*	5797*	33506*	1980	27709*	5797*	33506*

* Excludes live crocodile purchases (see Tables 2-31 – 2-34)

corrected values reported herein. In some instances the differences appear to be minor, but in one instance (the 1974 C. novaeguineae harvest) there is an egregious doubling of the actual value. I assume that the figures reported by him for the 1968-1969 to 1972-1973 period represent fiscal year (July-June) totals. From 1973 on he used calendar year exports, as I have throughout this study. The pre-1969 harvest figures in that paper are admittedly speculative and their degree of accuracy is impossible to ascertain, although they do not seem unreasonable to me.

Similarly, the harvest figures presented by Whitaker (1980:45-46) and Whitaker and Kemp (1981:23 and 25) are largely inaccurate. They were based on preliminary tabulations, after which additional records were available. The correct values for the appendices in these reports may be obtained from the data in this study.

There are several other sources of PNG crocodile harvests not reflected in this study. From 1969-1975 an unknown number (2,000-3,000?) of crocodiles (mostly C. novaeguineae) of unknown population structure were caught live in Western Province and sold to government demonstration farms. From 1976-1980 a further unknown number (5,000-10,000) of primarily juvenile C. novaeguineae were caught live and placed on village ranches in Western Province. This also occurred, to a lesser extent, in Gulf Province and, perhaps to a greater measure, in East Sepik

Province. During that same period, compensation claims of kina (about US$7) were paid to villagers in East Sepik Province for oversize crocodiles (> 20" belly width) inadvertently or intentionally killed. The total number and composition of animals thus 'bountied' could not be obtained, but I believe it to be between 500-1,500 This harmful practice was eventually discontinued in the early 1980's.

Data Limitations and Assumptions

Although data for the years 1973-1980 are complete, only about 60% of the 1972 data are represented, while data for 1969-1971 were largely unaccounted for. Data for earlier years were less accessible still, and correspondingly more difficult to quantify. Records were shifted among several governmental departments over the years and their maintenance suffered as a consequence.

The size class compositions shown herein are assumed to be representative of the populations at large with the following exceptions. Bias exists in the number of animals > 20" belly width harvested during 1972-1975 since illegal transhipment of oversize animals from Western Province to the Sepik provinces occurred (pers. comm. from pilots and Lake Murray hunters). Second, the largest size class thereafter (20") is disproportionally represented through the inclusion of oversize skins that were shrunken to meet legal requirements. Third, a marketing bias existed against skins < 8" belly width and they are thus unrepresented. For example, three buyers handled > 95% of Western Province skins during 1979: Daru Trading (CE81), Laki Trading (CE71), and Wildlife Division (CE65). As a matter of policy, CE81 did not purchase skins < 7", CE bought live crocodiles but not skins < 8", and < 5% of CE71's Western Province records (N = 4,678) were < 6". Lastly, hunter selection against harvesting small crocodiles is presumed to have occurred in New Britain and North Solomons provinces where rearing/holding facilities did not exist.

Exporters and Recent Evolution of the Industry

All but a negligible portion of the data in this study (<0.1 %) stem from the harvest of wild animals, although the production of crocodile skins from commercial ranches now forms a significant part of the annual trade in PNG. While approximately 80 exporters were known to be licensed during the 1969-1980 period (Table A-1, Appendix A), the bulk of the trade in any given year lay in the hands of only a few licensees. In fact, by 1980 a single license holder was responsible for more than 40% of the total exports.

Several important events occurred in response to the compilation of these data. The difficulties encountered provided the impetus for the establishment of a secure computerized data base for these and future records within the Wildlife Division. They also drew attention to the inadequacy of existing documentation of the trade. Accordingly, standardized purchase dockets were designed and subsequently issued free to each export license holder. These forms better addressed the biological needs of management, yet simultaneously allowed confidentiality of financial transactions desired by licensees. Furthermore, the harvest record summaries of this study provided persuasive quantitative evidence of the economic wastage in the trade of very small crocodile skins and contributed to the introduction of a lower size limit in 1981.

Following the successful shift of management policy toward the purchase of small live crocodiles for rearing and the establishment of large scale commercial ranches during the late 1970's and early 1980's, FAO terminated its involvement in the PNG crocodile project. A Crocodile Advisory Board, consisting of various government and industry representatives, was formed to help fill that void.

Within little more than a decade the crocodile skin industry in PNG was transformed from a troubled, unregulated industry with a suspect future to one of a competently managed resource that continues to assure the economic livelihood of many rural people while maintaining healthy populations of both crocodile species.

CHAPTER 3

HARVEST PATTERNS OF NEW GUINEA (*Crocodylus novaeguineae*) AND SALTWATER (*C. porosus*) CROCODILES IN PAPUA NEW GUINEA, 1969-1980

Introduction

For several decades the New Guinea (*Crocodylus novaeguineae*) and saltwater (*C. porosus*) crocodiles have been exploited as species of primary economic importance throughout lowland rural areas in Papua New Guinea (PNG; Fig. 3-1). There is no closed season or limit on the number of crocodiles that may be taken, although there are size restrictions on animals harvested for economic gain. Despite a year round open season, most hunter effort occurs during the dry season in periods of little or no moonlight when population densities are greater and animals are more susceptible to capture (Hall, 1983).

The legislative aspects of crocodile management in PNG commenced in 1969 with the enactment of the 1966 Crocodile Trade (Protection) Act, which mandated that all individuals engaged in the buying or exporting of crocodile products be licensed by the Wildlife Division (Department of Lands, Surveys, and Environment) in order for such commerce to be legal. With that Act, a maximum size limit of 51 cm

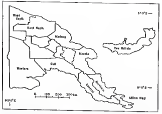

Figure 3-1. Map of Papua New Guinea indicating provinces of crocodile harvest mentioned in text, excluding Manus (2°0'S, 147°0'E), New Ireland (3°0'S, 151°30'E) and the North Solomons (6°0'S, 155°0'E). Right border of map is 153°E. Papuan Region provinces include: Western, Gulf, Central, and Milne Bay. The remaining labelled provinces are part of the New Guinea Region.

commercial belly width (see METHODS) was imposed on skin trafficking for both crocodile species. Political opposition led to the repeal of the 51 cm clause in the Sepik and Madang provinces until early 1975, when it was reinstated. Since that time, the upper size limit restriction has been uniform throughout PNG. Additionally, under the 1966 law skin shipments were made subject to inspection by enforcement officers. Further still, a requisite of licensing stipulated that buyers file individual quarterly returns on their purchases and that exporters first secure written authorization from the Wildlife Division prior to export of any consignment of live crocodiles or crocodile skins. Subsequent legislation led to the introduction of a minimum size skin limit of 18 cm, effective as of 15 February 1981 (Parker, 1981). Other reviews of the history of crocodile exploitation in PNG and government policies toward this resource have been presented elsewhere (Downes, 1971, 1973; Bolton, 1980; Bolton and Laufa, 1982; Hollands, 1987).

As part of an FAO (Food and Agricultural Organization of the United Nations) monitoring effort on biological investigations of PNG crocodiles, I compiled harvest data on these species during 1980-1981 (CHAPTER 2). My initial review of the data base indicated major flaws in the collection and tabulation process. Forms submitted by buyers and exporters were ill-suited for the compilation of biologically meaningful data and hence were left to accumulate without being analyzed once shipments were inspected and approved. Some of these problems have subsequently been overcome (Hollands, 1984, 1987). The present data set is an interpretation of these harvests prior to reforms initiated to ensure an adequate information retrieval system, and it highlights some of the difficulties associated with such data.

My objectives in examining these data were: (1) to determine the size, composition, and origin of PNG crocodile harvests by species; (2) to detect whether patterns and long-term trends occurred within and among populations of each species; and (3) to assess the biological and economic impacts of harvesting on the crocodile resource. In essence, this research sought to learn if existing legislation and policies were practicable and if they provided adequate safeguards to ensure sustainable yields to rural people who relied on crocodiles as a basis for their cash economy.

Methods

Harvest data for 1969-1980 were compiled from licensed dealer export permits on file at Wildlife Division headquarters in Waigani, National Capital District (9°30'S, 147°11'E). Data were tabulated on a calendar-year basis by the exporters date of application as that most closely paralleled the ties of harvest. Variables recorded were: exporter, date of application, provincial origin of purchases, species, skin type (dorsal incision = belly skin, ventral incision = hornback), skin size, and number of skins in each size class. Hide counts were tabulated into size classes as recorded by commercial belly width (BW, which is approximately 70% of the chest girth; see Parker, 1981) These original data were grouped in one inch (2.54 cm) BW increments as specified by existing regulations, and ranged from 4 - 20 inches (10 - 51 cm) BW. In this study, a correction of 4.4% was made for observed shrinkage in hides (N = 34, SE = 0.46) to derive preskinning belly width size classes, which were then transformed to equivalent total length (TL) measurements. Transformations for *C. novaeguineae* follow Montague (1984b; equations 10-12, 39-40; (note that equation 39 should have an SVL range of 13-99 cm, not 13-50 cm - Montague, in litt.]). The conversion of belly width to total length measurements for PNG *C. porosus* follows Whiteside (1978; $y = 3.5 + 4.05 x$). Prior to 1969, few data were available for trade in crocodile skins, and they permitted only limited interpretation.

In addition to skins, live crocodiles were purchased by Wildlife Division demonstration crocodile farms for resale as stock to large-scale commercial crocodile ranches. A breakdown of live crocodile purchases in 1979 and 1980 was obtained from government-station purchase dockets issued at

Angoram (4'01'S, 144'01'E; East Sepik Province), Babea (7'01'S, 141'30'E; Western Province), Balimo (9'04'S, 142'59'E; Western Province), Green River (3'54'S, 141'11'E; West Sepik Province), Kikori (7'27'S, 144'14'E; Gulf Province), Moitaka (9'30'S, 147'11'E; Central Province), and Pagwi (4'01'S, 143'0'E; East Sepik Province).

Sex determination of hides was not possible since crocodilians, except some adult male gharials (*Gavialis gangeticus*), do not exhibit secondary sexual characteristics other than size dimorphism (Rao, 1991). Size dimorphism is not apparent in PNG crocodiles under 2.7 m TL and 3.5 m TL for *C. novaeguineae* and *C. porosus*, respectively. Thus, except for a few individuals listed in Table 3-11, size dimorphism cannot be used as a basis for gender identification of the data in this paper. Data on *C. novaeguineae* sex ratios were collected by cloacal examination (Chabreck, 1963) of caught wild animals placed in rearing pens at Angoram in East Sepik Province (northern population) and in two subdistricts of Lake Murray District in Western Province (southern population; Fig. 3-2). The latter stock were sampled at Kavianenga (7'36'S, 141'19'E) and Komovai (7'33'S, 141'15'E) in the Middle Fly subdistrict and at Boikumeva (7'23'S, 141'23'E), Egiza (6'51'S, 141'30'E), Kapikam (6'43'S, 141'45'E), Magipopo (6'50'S, 141'27'E), Tagum (7'04'S, 141'34'E), Upovia (6'40'S, 141'27'S), and Wemak (Boimbulavu [6'50'S, 141'26'E])

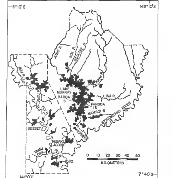

Figure 3-2 Middle Fly (left) and Lake Murray (right) subdistricts in the Lake Murray District, Western Province, Papua New Guinea

villages in the Lake Murray subdistrict, including the government crocodile farm at Baboa. Early Baboa data were compiled from station files. Due to a paucity of data, sex ratios were estimated for *C. novaeguineae* between 177-214 cm TL (Table 3-3) and for all *C. porosus* up to 218 cm TL. The sex ratios of these species were arbitrarily assumed to be similar, and mean value estimates for BW size class subgroups (4-6", 7-10", 11-14", 15-20") of the former species were applied to the latter species (Table 3-4). This was essential in order to calculate the sex-based age class distributions for further analysis (Tables 3-6 and 3-9) following the assignment of sizes to age classes (Table 3-5). That methodology is detailed in Appendices B and C.

The estimated age-size relationships for *C. novaeguineae* (Table 3-5) are based on my interpretation of unpublished growth data. Growth data for PNG *C. porosus* were lacking and the age-size relationships for that species (Table 3-5) were derived from a model for Australian *C. porosus* (Webb et al., 1978).

Harvest mortality tables (Tables 3-6 and 3-9), patterned after dynamic composite life tables (Caughley, 1977; Seber, 1982), were constructed from pooled harvest data where the number dying per age class (d_x) represents actual summed harvest. Those data were used to back-calculate the number alive at the beginning of each age class (l_x) and to estimate overall hunting mortality (q_x).

For certain analyses, the data were subdivided into three size classes: juveniles (<1.5 m TL), subadults (1.5 - 1.8 m TL for *C. novaeguineae*; 1.5 - 2.2 m TL for *C. porosus*), and adults (1.8 - 2.2 m TL for *C. novaeguineae* only). Size class structure was expressed by proportion because of the immeasurable interaction of factors that influenced numerical harvest. Binomial proportions tests (Z-statistic; Mendenhall, 1968) were used to test the null hypothesis that the proportions of juveniles, subadults, and adults were the same among populations for within-year comparisons (Tables 3-7 and 3-10). In this instance and elsewhere (size class trend analysis) the significance levels (P values) were adjusted by using Bonferoni's inequalities (Snedecor and Cochran, 1980) because the proportions were interdependent.

I used the Mann-Kendall test (Bradley, 1968) to test for the existence of trends (increase or decrease) in numerical harvests and the Kendall Tau test (Sokal and Rohlf, 1973) to detect trends among the frequency of harvest size classes. Where trends were detected, I regressed the size class proportions against the time of harvest (year number) to obtain the predicted proportions and their respective residuals. The number of positive and negative residual values were then tabled against successive year numbers of harvest and analyzed by chi-square contingency tests (2 x 2, 2 x 3, 2 x 4) to evaluate if the data showed cyclic periodicity.

Results

Total harvest figures were unobtainable for most years. Files for the years 1969-1971 were incomplete on a nation-wide basis (either lost or destroyed). A similar situation existed for 1972 data from the Sepik Provinces only. Complete files existed for the remainder of the period, but from 1973 to 1980 large portions of the national harvest were not identifiable as to province of origin for certain years (Tables 3-1 and 3-2).

Although few data from 1969-1972 were available for analysis, the total crocodile harvest for that period was known, though it was not identifiable as to species, origin, or size. Crocodile exports totaled 27,094 and 29,468 for 1969 and 1970, respectively (Wildlife Division file 14-9-19, part 1), while exports for 1971 and 1972 were 21,135 and 45,185 (Post Courier News, Port Moresby, PNG; 2 June 1973).

Similarly, some data were available for years prior to 1969, but the species and size distributions were not known. A single exporter (Booth & Co.) purchased a total of 112,505 PNG crocodile hides during 1959-1968 (Wildlife Division file 14-9-19, part 1). This figure provides some insight into the magnitude of unregulated harvest (pre-1969) as it is equal to one-fourth of the total for all licensed exports

Table 3-1. Crocodylus novaeguineae harvests in Papua New Guinea, 1969-1980. See METHODS for data source.

ORIGIN	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979*	1980*	TOTALS
Papua Region													
Western Province	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Gulf "	--	--	--	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	--	[illegible]	[illegible]	[illegible]
Central "	--	[illegible]	--	--	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	--	[illegible]	[illegible]	[illegible]
Mixed Papuan	--	--	--	2637	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Region subtotal	[illegible]	2351	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
New Guinea Region													
Sepik Provinces	--	--	--	[illegible]	[illegible]	4115	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Madang "	--	--	--	[illegible]	--	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Morobe "	[illegible]	--	--	--	--	--	--	--	--	--	--	[illegible]	[illegible]
Mixed New Guinea	--	--	--	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	--	[illegible]	--	[illegible]
Region subtotal	[illegible]	--	--	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Unidentified	--	--	--	--	[illegible]	[illegible]	--	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Totals	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

* Includes animals harvested alive but not exported

Table 3-2 *Crocodylus porosus* harvests in Papua New Guinea, 1969-1980. See METHODS for data source.

ORIGIN	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979*	1980*	TOTALS
Papua Region													
Western Province	777	85	20	7777	7753	7774	702	7037	746	857	107	732	7075
Gulf "	--	--	--	27	7	707	17	30	50	--	107	277	777
Central "	--	--	--	--	357	777	709	787	700	--	0	477	7777
Mixed Papuan	--	--	--	337	7778	7507	875	770	877	7707	7938	477	10763
Region subtotal	117	87	20	1477	7775	3567	2720	2704	2157	7070	2747	2474	22077
New Guinea Region													
Sepik Provinces	--	--	--	770	4780	2079	4763	2774	2777	2752	7750	2935	78770
Madang "	--	--	--	0	--	133	0	--	777	--	107	70	471
Morobe "	23	50	-	--	--	--	--	--	--	--	--	577	873
Northern "	--	--	--	--	--	12	--	77	--	--	--	70	70
Mixed New Guinean	--	--	--	7034	2777	7770	77	7	733	750	787	--	7775
Region subtotal	23	50	--	7772	7770	2753	4754	2777	2753	3002	7857	7570	35035
Island Region													
New Britain	--	--	--	--	--	--	--	--	--	772	505	777	1477
North Solomons	--	--	--	--	--	77	--	-	--	--	--	--	77
Unspecified	--	--	--	--	--	777	--	907	887	778	7737	7077	8775
Totals	754	127	70	1880	77757	7277	6074	6357	6670	7757	7707	7077	66477

* Includes animals harvested alive but not exported

from 1969-1980 (445,776). The provincial origin of these pre-1969 hides was as follows: Milne Bay - 2,318; Western - 51,488; Western/Gulf - 26,005; Gulf - 2,319; Central - 2,823 (Papua Region subtotal = 84,953); Sepik - 27,243; Manus - 309 (New Guinea Region subtotal = 27,552).

C. novaeguineae

Export file records for PNG harvests of *C. novaeguineae* totaled 281,027 (annual $\overline{x}$ = 31,225) for 1972-1980, the years for which data were largely complete. Of this total, 50.9% (annual $\overline{x}$ = 15,899) was from the Papua (southern) Region and 38.8% (annual $\overline{x}$ = 12,127) from the New Guinea (northern) Region, with 10.2% of unknown origin (Table 3-1). Since Western and the Sepik Provinces each comprised more than 80% of the harvest identifiable as to origin in their regions (Papua and New Guinea, respectively), data for *C. novaeguineae* from those provinces were considered to be broadly representative and were used for geographic comparisons (Figs. 3-3 and 3-4).

Excluding hides of unknown origin, these data indicated a minimum mean annual crop for Western Province of 8,292 animals with an average size of 142 cm TL (23.8 cm BW). Based on discussion with skin buyers and exporters, 70% of that total was believed to have originated from Lake Murray District (Fig. 3-2); most of the remainder was from the Aramia-Bamu River basins in southeastern Western Province

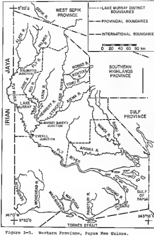

Figure 3-3. Western Province, Papua New Guinea.

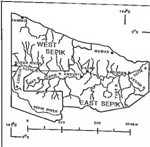

Figure 3-4. Sepik Provinces, Papua New Guinea.

Table 3-3. Commercial belly width size classes for Crocodylus novaeguineae, estimated equivalent total length measurements, numbers of individuals harvested per size class, sex ratios and associated sample sizes.

Belly width (inches)	Est. total length (cm)	Number harvested Western Province	Number harvested Sepik Provinces	Sex ratio male	Sex ratio female	N
4	57-67	5696	13110	0.30	0.70	(79)
5	68-79	7773	13797	0.40	0.60	(153)
6	80-90	14140	12109	0.38	0.62	(144)
7	91-129	11902	10376	0.50	0.50	(143)
8	130-136	8116	5840	0.51	0.49	(152)
9	137-142	6500	4687	0.50	0.50	(128)
10	143-149	5117	3210	0.49	0.51	(147)
11	150-156	3657	2251	0.58	0.42	(161)
12	157-163	2943	1979	0.60	0.40	(134)
13	164-169	2291	1659	0.50	0.50	(144)
14	170-176	2173	1586	0.53	0.47	(70)
15	177-183	2060	1745	0.70	0.30	(30)
16	184-189	2120	1681	"	"	est.
17	190-196	1960	1557	"	"	"
18	197-201	1790	1487	"	"	"
19	202-208	1504	1204	"	"	"
20	209-214	1515	1011	"	"	"
Totals		81257*	79310**			

* Excludes 37 animals > 2.2 m TL harvested in 1969 (see Table 3-11)

** Excludes 816 animals > 2.2 m TL harvested from 1972-1975 (see Table 3-1

Table 3-4 Commercial belly width size classes for *Crocodylus porosus*, estimated equivalent total length measurements, numbers of individuals harvested per size class, and estimated size class sex ratios.

Belly width (inches)	Est. total length (cm)	Number harvested Papua Region	New Guinea Region	Island Region	Est. sex ratio male	female
4	36-46	3591	5853	61	0.37	0.63
5	47-57	4161	5646	119	"	"
6	58-68	4424	5973	141	"	"
7	69-79	3249	4672	153	0.50	0.50
8	80-89	2128	3201	177	"	"
9	90-100	1522	2456	173	"	"
10	101-111	1045	1549	153	"	"
11	112-122	684	1135	117	0.56	0.44
12	123-132	487	883	100	"	"
13	133-143	346	816	81	"	"
14	144-154	318	479	87	"	"
15	155-165	274	418	87	0.70	0.30
16	166-175	215	345	50	"	"
17	176-186	145	297	30	"	"
18	187-197	114	288	42	"	"
19	198-208	107	293	48	"	"
20	209-218	184	319	65	"	"
Totals		22994*	34401**	1664		

* Excludes 3 animals > 2.2 m TL harvested in 1969 (see Table 3-11).
** Exludes 824 animals > 2.2 m TL harvested during 1972-1975 (see Table 3-11).

Table 3-5. Estimated age (years) and size classes (cm total length) of Papua New Guinea crocodiles.

	C. novaeguineae		*C. porosus*	
Age class	Est. size class male	female	Est. size class male	female
0-1	≤ 57	≤ 57	≤ 75	≤ 75
1-2	58-84	58-80	76-114	76-107
2-3	85-108	81-98	115-140	108-130
3-4	109-130	99-114	141-160	131-145
4-5	131-150	115-128	161-180	146-160
5-6	151-166	129-142	181-200	161-175
6-7	167-182	143-154	201-218	176-190
7-8	183-196	155-166		191-205
8-9	197-208	167-176		206-215
9-10	209-214	177-186		216-218
10-11		187-194		
11-12		195-202		
12-13		203-208		
13-14		209-214		

(Fig. 3-3). Mean annual harvest of C. novaeguineae in Western Province for the period 1956-1970 was estimated at 7,000 (Whitaker, 1980). Analysis of 1966-1967 data (regarded as the peak of historical exploitation; from Bustard, 1967) revealed a mean skin size of 181 cm TL, (35.1 cm BW), with 16.2% of the sample > 2.2 m TL. The average skin size for that interval was presumed to have been larger than that for the more recent period due to a selective bias by hunters and buyers against < 0.8 and > 2.2 m TL size classes during 1969-1980. When those size classes are omitted, mean skin size was similar for both periods 162 cm TL (31.7 cm BW) for 1969-1980 versus 172 cm TL (35.7 cm BW) for 1966-1967.

Data for the Sepik Provinces showed a larger numerical harvest than for Western Province; however, the size at harvest was very similar. The minimum mean annual harvest for 1972-1980 was 8,903 with an average skin size (excluding animals > 2.2 m TL) of 135 cm TL (21.0 cm BW). Mean sample skin size for 1966-1967 was 134 cm TL (20.7 cm BW, all size classes), with only 1.1% > 2.2 m TL.

Hunting mortality in Western Province (20.2%) was significantly lower (Z = -34.9, P < 0.001) than that in the Sepik Provinces (23.5%) (Table 3-6).

Harvest data were complete for the years 1973-1980 and no trend in numerical harvest was detected for total national harvests in that period (Mann-Kendall test, P >

Table 3-6. Harvest of *Crocodylus novaeguineae* in Western and Sepik Provinces, Papua New Guinea (pooled data, 1969-1980). See Appendices B and C for conversion factors used in calculating sex-based age class distributions.

Age class (years)	Number harvested				Total harvested (d_x)		Minimum alive at beginning (l_x)	
	Western Province		Sepik Provinces					
	male	female	male	female	Western Province	Sepik Provinces	Western Province	Sepik Provinces
0-1	155	362	358	836	517	1194	81257	79310
1-2	7105	9086	11191	17317	16191	28508	80740	78116
2-3	5677	9191	4904	7890	14868	12794	64549	49608
3-4	3796	2441	3219	2128	6237	5347	49681	36814
4-5	9608	2136	6656	1862	11744	8518	43444	31467
5-6	4157	7379	2721	5338	11536	8059	31700	22949
6-7	2961	3707	2302	2312	6668	4614	20164	14890
7-8	3062	2189	2442	1477	5251	3919	13496	10276
8-9	2306	1594	1884	1160	3900	3044	8245	6357
9-10	1061	936	708	776	1997	1484	4345	3313
10-11		738		586	738	586	2348	1829
11-12		769		631	769	631	1610	1243
12-13		387		309	387	309	841	612
13-14		454		303	454	303	454	303
Totals	39888	41369	36385	42925	81257	79310	402874	337087

Harvest mortality rate (d_x / l_x) = 0.2017 0.2353

0.05). Regional numerical harvests could not be so evaluated due to the large numbers of animals of unidentified origin.

However, when the frequencies of harvest size class compositions were examined, some trends were detected in Western Province during the 1969-1980 interval. Juveniles showed an increase in proportional harvest composition while the adult size class experienced a decrease (Kendall Tau test, $P < 0.05$ for both).

Comparative data among populations existed only for the years 1972-1980 (Fig. 3-5). During that period no trends in harvest composition were detected for Western Province harvests, while a decreasing trend in the subadult size class was detected in harvests from the Sepik Provinces (Kendall Tau test, $P < 0.05$). Cyclic periodicity was absent in all but the Western Province juvenile size class for which a 3 year pattern existed ($X^2 = 6.00$, 2 df, $P < 0.05$). Significant differences in size class proportions were found in most within-year comparisons among populations (Table 3-7).

The proportion of male to female juvenile and subadult C. novaeguineae ($N = 1,777$) in Lake Murray District, Western Province (Table 3-8) was the same among sample years ($Z = 0.48$, $P > 0.05$) with a 1:1 sex ratio for 1969 ($Z = 0.41$, $P > 0.05$) and 1980 ($Z = 0.45$, $P > 0.05$). However, both the Lake Murray (male biased) and Middle Fly (female biased)

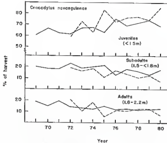

Figure 3-5. Harvest structure of Crocodylus novaeguineae in Papua New Guinea, 1969-1980. Solid line = Western Province; dashed line = Sepik Provinces.

Table 3-7. Pairwise comparisons of Crocodylus novaeguineae harvests from the Western and Sepik Provinces, Papua New Guinea. Size classes expressed as proportions of yearly samples (in parentheses). Differences are significant at * P < 0.05, or ** P < 0.001 (binomial proportions test; Mendenhall, 1968), NS, not significant.

YEAR	PROVINCE	JUVENILES < 1.1 m	SUBADULTS 1.1 - < 1.1 m	ADULTS 1.1 - 2.1 m
[illegible]	Western	[illegible] ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])
	Sepik	----	----	----
[illegible]	Western	[illegible] ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])
	Sepik	----	----	----
[illegible]	Western	[illegible] ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])
	Sepik	----	----	----
[illegible]	Western	[illegible] NS ([illegible])	[illegible] ** ([illegible])	[illegible] ([illegible])
	Sepik	[illegible] ([illegible])	[illegible] ([illegible])	[illegible] ** ([illegible])
[illegible]	Western	[illegible] ([illegible])	[illegible] ** ([illegible])	[illegible] ** ([illegible])
	Sepik	[illegible] ** ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])
1974	Western	[illegible] ** ([illegible])	[illegible] * ([illegible])	[illegible] ([illegible])
	Sepik	[illegible] ([illegible])	[illegible] ([illegible])	[illegible] ** ([illegible])
1975	Western	[illegible] ([illegible])	[illegible] ** ([illegible])	[illegible] ** ([illegible])
	Sepik	[illegible] ** ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])
[illegible]	Western	[illegible] ** ([illegible])	[illegible] ([illegible])	[illegible] * ([illegible])
	Sepik	[illegible] ([illegible])	[illegible] ** ([illegible])	[illegible] ([illegible])
1977	Western	[illegible] ([illegible])	[illegible] ** ([illegible])	[illegible] ** ([illegible])
	Sepik	[illegible] ** ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])
[illegible]	Western	[illegible] ([illegible])	[illegible] ** ([illegible])	[illegible] ([illegible])
	Sepik	[illegible] ** ([illegible])	[illegible] ([illegible])	[illegible] NS ([illegible])
1979	Western	[illegible] ([illegible])	[illegible] NS ([illegible])	[illegible] ([illegible])
	Sepik	[illegible] NS ([illegible])	[illegible] ([illegible])	[illegible] NS ([illegible])
[illegible]	Western	[illegible] ([illegible])	[illegible] ** ([illegible])	[illegible] ** ([illegible])
	Sepik	[illegible] ** ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])
TOTALS	Western	[illegible] ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])
	Sepik	[illegible] ([illegible])	[illegible] ([illegible])	[illegible] ([illegible])

Table 3-8. Sex ratios of caught wild crocodiles reared in captivity in the Lake Murray District, Western Province, and at Angoram, East Sepik Province, Papua New Guinea

Year	Area	Number of males (%)	Number of females (%)
	C. novaeguineae		
1969	Baboa	149 (51.2)	142 (48.8)
1980	Lake Murray subdistrict	511 (53.9)	437 (46.1)
	Middle Fly subdistrict	219 (40.7)	319 (59.3)
	Subtotal	730 (49.1)	756 (50.9)
	Total Lake Murray District	879 (50.5)	898 (49.5)
1981	Angoram	11 (25.0)	33 (75.0)
	C. porosus		
1980	Lake Murray District	14 (26.4)	39 (73.6)

subdistrict samples differed, in an inverse manner, from a 1:1 ratio ($Z = 2.39$, $P < 0.01$, $Z = 4.23$, $P < 0.001$) as well as from each other ($Z = 4.89$, $P < 0.001$). Meanwhile, a female bias was observed for a small sample of the northern population at Angoram on the Sepik River ($Z = -2.87$, $P < 0.005$). No data were available for adult *C. novaeguineae*.

Although the composite sex ratio for Lake Murray *C. novaeguineae* indicated the existence of an equal proportion of males to females, there were generally significant departures from unity within size classes (Table 3-3)

C. porosus

Total export file records for PNG harvests of *C. porosus* from 1972-1980 was 66,164 (annual $\bar{x} = 7,352$); 52.8% originated from the New Guinea Region (annual $\bar{x} = 3,883$), 2.5% from the Island Region (annual $\bar{x} = 435$) origin, 34.4% from the Papua Region (annual $\bar{x} = 2,531$), and 10.1% of unknown locations (annual $\bar{x} = 1,117$) (Table 3-2). The average size at harvest (excluding animals > 2.2 m TL) was 83 cm TL (19.6 cm BW) in the New Guinea Region, 113 cm TL (27.0 cm BW) in the Island Region, and 81 cm TL (19.1 cm BW) in the Papua Region

Hunting mortality rates in the Papua Region (59.7%) and New Guinea Region (56.6%) were similar, but statistically different ($Z = 9.64$, $P < 0.001$). However, hunting mortality in the Island Region (35.0%) was significantly lower than either the Papua Region ($Z = 32.4$, $P < 0.001$) or New Guinea Region ($Z = 28.8$, $P < 0.001$) (Table 3-9). Hunting mortality for combined *C. porosus* populations (56.8%) was significantly greater than that for *C. novaeguineae* (21.7%) ($Z = 241.5$, $P < 0.001$).

As with *C. novaeguineae*, no trend was found in *C porosus* for the 1973-1980 numerical national harvests (Mann-Kendall test, $P > 0.05$). Unlike the case for the former species, no trends or cyclic patterns were detected in *C. porosus* size class compositions (Kendall Tau test, $P > 0.05$) (Fig. 3-6). Also as for *C. novaeguineae*, most within-year comparisons among populations revealed significant differences in harvest size class proportions (Table 3-10).

Few data ($N = 53$) were available for juvenile and subadult *C. porosus*, but they indicated a 0.6:1 male-female sex ratio ($Z = -3.03$, $P < 0.005$) in Lake Murray District of the Papua Region (Table 3-8).

Harvesting of all sizes of animals of both species was practiced in the New Guinea Region until 1975. Partial 1972 data were available as well as complete data for 1973-1975. Estimates of size/age class and sex ratios were not derived for crocodiles > 2.2 m TL to obtain estimated harvest mortality rates for such individuals, but such data indicate that minimum totals of 1,410 *C. novaeguineae* ($\bar{x} = 240$ cm TL)

Table 3-9   Harvest of *Crocodylus porosus* in the Papua, New Guinea, and Island Regions, Papua New Guinea (pooled data, 1969-1980, Island Region 1978-1980 only)   See Appendices B and C for conversion factors used in calculating sex-based age class distributions.

Age class (years)	Number harvested Papua Region male	Papua Region female	New Guinea Region male	New Guinea Region female	Island Region male	Island Region female	Total harvested (d_x) Papua Region	New Guinea Region	Island Region	Minimum alive at beginning (l_x) Papua Region	New Guinea Region	Island Region
0-1	1549	1711	1611	11611	100	211	11113	10614	619	21911	11101	1604
1-2	1111	2101	1411	1111	911	953	1101	1107	119	9751	17951	1115
2-3	111	661	1111	1915	111	111	1151	1162	251	1960	5119	196
3-4	711	191	521	101	91	52	159	119	119	2911	1911	119
4-5	991	157	160	131	16	61	119	105	197	1946	1011	106
5-6	151	161	171	191	59	21	257	111	11	601	1211	109
6-7	111	55	111	120	79	34	111	111	91	341	711	119
7-8		19		119		19	15	119	19	102	231	11
8-9		17		91		17	11	11	11	91	121	33
9-10		17		29		9	11	11	9	11	29	9
Totals	19115	11101	11106	10115	171	719	21011	14111	1664	19197	99101	4160
							Harvest mortality rate (d_x/l_x)			0.1171	0.1601	0.1111

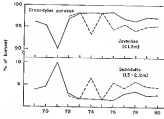

Figure 3-6. Harvest structure of *Crocodylus porosus* in Papua New Guinea, 1969-1980. Solid line = Papua Region; dashed line = New Guinea Region.

Table 3-10 Pairwise comparisons of Crocodylus porosus harvest compositions from the Papua and New Guinea Regions, Papua New Guinea. Size classes expressed as proportions of yearly samples (in parentheses). Differences are significant at * P < 0.05, or ** P < 0.001 (binomial proportions test; Mendenhall, 1968); NS, not significant

YEAR	REGION	JUVENILES < 1.0 m	SUBADULTS 1.0 - 2.2 m
1969	PAPUA	0.9515 (125)	0.0154 NS (4)
	NEW GUINEA	1.0000 NS (11)	----
1970	PAPUA	0.9515 * (51)	0.0482 (1)
	NEW GUINEA	0.9478 (40)	0.1810 * (8)
1971	PAPUA	0.9000 (18)	0.1000 (2)
	NEW GUINEA	----	----
1972	PAPUA	0.9685 (1345)	0.0111 * (44)
	NEW GUINEA	0.9755 * (2151)	0.0112 (51)
1973	PAPUA	0.9811 (1880)	0.0188 NS (73)
	NEW GUINEA	0.9814 NS (7295)	0.0186 (121)
1974	PAPUA	0.9811 ** (1585)	0.0179 (51)
	NEW GUINEA	0.9141 (1005)	0.0657 ** (210)
1975	PAPUA	0.9510 (1155)	0.0180 NS (40)
	NEW GUINEA	0.9515 NS (4515)	0.0154 (77)
1976	PAPUA	0.9547 ** (2569)	0.0151 (40)
	NEW GUINEA	0.9450 (2555)	0.0550 ** (151)
1977	PAPUA	0.9555 * (8055)	0.0305 (66)
	NEW GUINEA	0.8555 (1156)	0.0641 * (143)
1978	PAPUA	0.9547 ** (1575)	0.0151 (107)
	NEW GUINEA	0.9487 (3842)	0.0511 ** (140)
1979	PAPUA	0.9734 ** (2184)	0.0267 (80)
	NEW GUINEA	0.9554 (1756)	0.0444 ** (175)
1980	PAPUA	0.9714 (1409)	0.0284 NS (47)
	NEW GUINEA	0.9752 NS (1411)	0.0145 (87)
TOTALS	PAPUA	0.9781 (21444)	0.0218 (530)
	NEW GUINEA	0.9552 (11104)	0.0148 (1157)

and 624 *C. porosus* ($\bar{x}$ = 296 cm TL) > 2.2 m TL were harvested in that period (Table 3-11).

Discussion

Harvest Trends

Total annual harvest of PNG crocodiles is largely a reflection of hunting and marketing (domestic and international) conditions and wide variations existed among and within populations for these years. Hunter success is strongly influenced by water level, by availability of salt, batteries, electric torches, and food to hunters, and by access to skin buyers (Hall, 1983). Figures 3-7 and 3-8 illustrate the within and among year ranges in precipitation patterns that affected crocodile harvests.

The observed trends within and among these crocodile populations are artifacts of selective harvesting to satisfy market demand as well as natural dynamic flux. Such harvesting entailed selection for many thousands of very small (0.4 - 0.9 m TL) juveniles (primarily in the New Guinea Region populations), which were utilized as watch straps in the Singapore and Japanese markets. Meanwhile, selection against those sizes of animals occurred in the Papua Region. Voluntary conservation measures and marketing logistics in the latter region were responsible for that bias.

Table 3-11. Fooled harvest of *Crocodylus novaeguineae* and *C. porosus* > 2.2 m total length in Papua New Guinea during 1972-1975.

Belly width (Inches)	*C. novaeguineae* Est. total length (cm)	*C. novaeguineae* Number Harvested	*C. porosus* Est. total length (cm)	*C. porosus* Number Harvested
21	215-221	383	219-229	84
22	222-228	383	230-240	88
23	229-235	321	241-251	48
24	236-242	140	252-262	83
25	243-248	108	263-272	66
26	249-255	73	273-283	31
27	256-262	63	284-294	43
28	263-268	40	295-304	22
29	269-275	28	305-315	24
30	276-282	41	316-326	16
31	283-288	15	327-338	18
32	289-296	17	339-343	15
33	297-302	5	348-358	17
34	303-308	5	359-369	4
35	310-316	6	370-379	4
36	317-322	2	380-390	0
37	323-329	0	391-401	0
38	330-336	2	402-411	12
39	337-343	3	412-423	2
40	344-350	0	424-433	13
41	351-356	0	434-444	7
42	357-363	0	445-455	8
43	364-370	3 *	456-465	8
44	371-377	0	466-476	7
45	378-383	0	477-487	5
46	384-390	3 *	488-497	3
47			498-509	8
48			510-519	3
49			520-530	0
50			531-543	3
Totals		1447 **		823 ***

* Probably misidentified *C. porosus*
** Includes 37 animals harvested in Western Province during 1969
*** Includes 3 animals harvested in Western Province during 1969

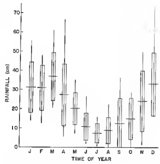

Figure 3-7. Means (horizontal lines) of monthly precipitation at Bomsett, Papua New Guinea, 1965-1980 (no 1968 data). Rectangles, standard deviations; vertical lines, ranges.

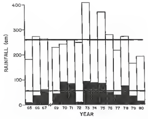

Figure 3-8. Annual precipitation patterns at Boesat, Papua New Guinea, 1965-1980 (no 1968 data). Shaded areas, dry season (June-October) totals; upper horizontal line = mean annual precipitation, lower horizontal line = mean dry season precipitation.

In 1969 an upper size limit of 51 cm BW (2.2 m TL) was introduced in the Papua Region. That law became uniform in the New Guinea Region in 1975 (animals > 2.2 m TL are excluded in Tables 3-3 - 3-10). The subsequent increase in the number of breeding adults significantly enhanced production in that area. I assume the sudden sustained shift in harvest structure of *C. novaeguineae* reflects the increased availability of young. A similar plateau leap in juvenile *C. novaeguineae* harvest occurred in Western Province in 1976. During that year a new exporter, Laki Trading, provided an outlet for watch strap' sized animals that reduced the selective bias against very small juveniles.

To counter the economic waste in trading of skins from small juveniles, a national buying scheme was introduced in 1979 to encourage the sale of small live crocodiles that could be reared to maximum profitable size in commercial facilities (Whitaker and Kemp, 1981). An immediate impact of that action was a minimum eleven-fold projected revenue increase from live animals bought during 1979 and 1980 (Hall, unpubl. data). It also reinforced the increased proportion of juveniles in the total harvest. Hide trafficking in animals less than 18 cm BW (1.0 m TL) became illegal in 1981 (Parker, 1981). Falsified purchase records were partly responsible for the huge increases of juvenile *C novaeguineae* harvest (and consequent depressed harvest of subadults and adults) in the Sepik during 1981 (F. Whitam, pers. comm.).

Other factors important in enhancing the economic return of the crocodilian resource were extension activities aimed at improving skinning and preservation techniques and the elimination of marketing less valuable hornback (ventral incision) hides. The latter formerly occurred in high numbers from the Sepik Provinces until the mid-1970's, but were uncommon elsewhere.

Harvest Mortality Rates

There are no implicit assumptions regarding the stability of population sizes in my calculations of harvest mortality rates (q_x) for hunted crocodile populations (Tables 3-8 and 3-9), nor do I assume that the distribution of the probabilities of age-specific mortality are the same for harvesting mortality as they are for all other sources of mortality combined. However, I believe that crocodile populations probably increased in response to conservation measures during the 1969-1980 interval. This statement is supported in part by the fact that the average harvested skin size of both species grew steadily larger during this period (CHAPTER 2), despite an increasing proportion of juveniles in the total harvest composition.

Furthermore, I assume that commercial harvesting represented the primary (but not only) cause of mortality for animals up to 2.2 m TL in hunted populations (except crocodiles < 2 years of age for which a selective bias against harvest existed - see below)

The degree to which harvesting was compensatory or additive is unknown and unaccounted for. Thus, my mortality estimates represent maximum, not absolute, values. The utility of such calculations lies in that their allowing comparative relative estimates of the impact of harvesting on populations within and among species.

A noted difference in the harvest of these species is that the percentage of juvenile C. porosus is enormously higher than that of C. novaeguineae; the juvenile to subadult harvest ratio is 31.9 to 1 in the former species versus 4.4 to 1 in the latter species. This fact is due in large part to the greater demand for hides of C. porosus. Skins of that species produce a superior leather as a result of their smaller belly scales and consequent greater pliability. Thus, they are worth about 25% more on the domestic market. To a lesser extent the disparate juvenile/subadult harvest ratio among species is a reflection of the differential number of size classes encompassed by such comparisons. However, although a much smaller proportion of C. porosus mature and breed below the maximum legal harvest size compared with C. novaeguineae, populations of C. porosus are exploited more intensively than those of C. novaeguineae, despite being afforded better relative protection with respect to adult size classes. The low hunting mortality rate for C. porosus observed in New Britain compared to mainland PNG populations is a reflection of the small number of 0-1 year age class animals represented in the harvest. I believe this to be attributable to marketing infrastructure in that area, although it in part may also reflect a real difference in population size structure.

A harvest feature common to both these species is the disproportionate number of individuals contained in the largest legal size class (see data for 20" BW row in Table B-1, Appendix B). Virtually all of these irregularities were attributable to a single exporter (Hall, unpubl. data) and are believed to be the result of illegal trafficking in oversized hides carefully shrunken to meet legal requirements.

PNG crocodile populations of animals < 2.2 m TL were perhaps subjected to annual harvest rates of 20 percent or more during the 1969-1980 interval with no apparent long term negative biological effects. Such rates may appear to be high and excessive to some critics of crocodilian trade practices. However, continuing research in the southeastern U.S. on recovered populations of American alligator (Alligator mississippiensis) compares favorably with the PNG experience. Studies designed to test the effects of a 50% removal rate of annual production (eggs and hatchlings) in several areas of northcentral Florida indicate that populations to date have not been adversely affected by such harvests (Jennings et al., 1988). Also, the fact that PNG harvests were heavily directed toward juvenile and subadult animals accords well with the life history strategies of crocodilians as these are the most expendable population segments (Magnusson, 1986).

Observed Sex Ratios

The sex of *C. porosus* and all other crocodilian species studied to date is known to be temperature-dependent during incubation (Ferguson and Joanen, 1982; Webb et al., 1983a; Webb and Smith, 1984; Lang, 1987). Presumably this is true for *C. novaeguineae* as well. If so, then differences in climate and microhabitat could be responsible for the observed inverse sex ratios of *C. novaeguineae* between the Middle Fly and Lake Murray subdistricts. Annual precipitation in the former area (Bosset = 258 cm; Hall, 1983) is considerably lower than in the latter (Babos = 306 cm, Pangoa = 325 cm, McAlpine, 1971; Hall, 1983). Whether possible differences also existed with respect to age/sex-specific mortality remains unknown.

Areas for Further Research

Most of the results described herein are rather straightforward and readily analyzed using data compiled by buyers during regulated business transactions. However, the estimation of harvest mortality rates (Tables 3-6 and 3-9) entails the use of accessory data on size/age-specific growth rates and size/age-specific sex ratios that are not obtainable without special, and more costly, effort. In order to derive baseline approximations of those values, I have had to sacrifice accuracy for precision and make compromising guesstimates with the best available data. To wit, growth and sex ratio data were either lacking or too limited to be useful for northern (New Guinea Region) *C novaeguineae* and for all PNG populations of *C. porosus*. Thus, data on growth and sex ratios for southern (Papua Region) *C. novaeguineae* were substituted as approximations for northern population estimates. Likewise, growth rates for PNG *C. porosus* populations had to be estimated by using data from Australian *C. porosus* populations, while sex ratio distributions for that species were assumed to be similar to southern PNG *C. novaeguineae* populations. Furthermore, the existing data base for southern PNG *C. novaeguineae* populations is also quite limited for individuals > 1.5 m TL. Clearly, additional investigation of intra- and inter-specific population growth rates and sex ratio compositions and their associated variances is called for to improve the pictures presented herein and the acquisition of such parameters should be part of crocodilian research programs everywhere.

The need for greater accuracy of data for the foregoing interpretations is best illustrated with respect to PNG populations of *C. novaeguineae*. Although the range of sizes harvested is similar between northern and southern populations, there are important differences among them. Southern *C. novaeguineae* are significantly larger at hatching and hatch over a much longer interval than do northern animals (Hall and Johnson, 1987). However, maximum verified sizes (TL) of male and female individuals are smaller for southern *C. novaeguineae* (3.31 m and 2.65 m, respectively; Hall and Johnson, 1987) than for their northern counterparts. A captive female at Pagwi, East Sepik Province measured 3.05 m (Jelden, 1985) while a record sized male of 3.47 m was recently found illegally killed in the Mamberamo River, Irian Jaya (the western, Indonesian, half of New Guinea) (S. Frazier, cited in Brazaitis et al., 1988). Additionally, and more importantly, subsequent to the compilation of the foregoing harvest date, it was found that the southern population of *C. novaeguineae* was morphologically distinct from the northern type population (Hall, 1989).

Summary

Although the PNG crocodile harvest has been sustained with no detectable long-term negative effects, the potential for further economic return from a manipulated harvest is enormous. Hall and Johnson (1987) found that 74% of nesting female *C. novaeguineae* in Western Province were smaller than the size protected by law. Accordingly, they recommended a reduction in the upper skin size limit to 40 cm BW (< 1.8 m TL) to enhance juvenile production. Cox (1985) also reported that significant proportions of breeding female *C. novaeguineae* (86%) and that some *C. porosus* were unprotected in the Sepik Provinces as well. Consequently, he made a similar suggestion to reduce the upper size trading limit as did Montague (1983).

In conclusion, differential harvesting and marketing strategies have probably acted upon regional populations of PNG crocodile species to make them appear more dissimilar than what they really are. These factors can largely account for trends detected in size structure within *C. novaeguineae* harvests and for differing intra- and inter-specific harvest mortality rates. Because of the very large sample sizes, the significant differences observed among intra-specific comparisons of harvest compositions are less meaningful biologically than they are statistically. This underscores the need for caution when interpreting this sort of data.

The people of PNG have had a long cultural affinity with crocodiles. That fact, coupled with large tracts of difficult access habitat, low density human populations, and recent management efforts (if continued) affords PNG crocodiles a positive conservation prognosis.

CHAPTER 4

ESTIMATION OF NESTING FEMALE CROCODILIAN SIZE FROM CLUTCH CHARACTERISTICS. CORRELATES OF REPRODUCTIVE MODE AND HARVEST IMPLICATIONS

Introduction

Although primarily pantropical in distribution (Sill, 1968), the order Crocodylia has several extant species with ranges that are in part north temperate (*Crocodylus acutus*, *C. moreletii*, *C. niloticus*, *C. palustris*, *Gavialis gangeticus*) or south temperate (*C. niloticus*, *Caiman latirostris*, *C. yacare*) (Neill, 1971; Groombridge, 1982). The surviving members of the genus *Alligator* (*A. mississippiensis* and *A. sinensis*) occur only in temperate climates and endure winter weather by constructing earthen dens where they become torpid in response to thermometabolic stress (McIlhenny, 1935; Brisbin et al., 1982).

In this paper, I examine morphometric aspects of nesting crocodilians, their modes of reproduction, and discuss environmental constraints experienced by temperate American alligators (*A. mississippiensis*) and tropical New Guinea crocodiles (*C. novaeguineae*). The former species is endemic to the United States and the latter to the island of New Guinea. References to *C. novaeguineae*, unless otherwise indicated, pertain to those populations south of the New

Guinea central highlands, as they compose a taxonomically distinctive form (Hall, 1989). Biologically meaningful data on reproductive female crocodilians are generally difficult to obtain compared to data on crocodilian nests and nest sites. Therefore, I sought to determine whether the latter type of data could be used to reconstruct demographic profiles of breeding crocodilian populations given data on small subsets of the nesting female segments. I also briefly consider the implications of harvesting on the reproductive demography of these populations.

Study Areas

Data on C. novaeguineae were collected during 1980-1981 in Lake Murray District, Western Province, Papua New Guinea (PNG; 7°00'S, 141°30'E) (Hall and Johnson, 1987; Hall, unpubl.). Additional data on nesting animals are from Cox (1985: Appendix 6). The Lake Murray area is primarily tropical moist forest (mean annual precipitation 3,200 mm) with pronounced wet (November-May) and dry (June-October) seasons. Habitats important for nesting crocodilians are the fringing mixed swamp/woodland forests, Echinochloa grass swamps, and Saccharum-Phragmites grass swamps. Further details are provided in CSIRO (1971) and Hall and Johnson (1987).

Observations on nesting alligators were made at Lacassine National Wildlife Refuge (NWR, 30°00'N, 92°50'W), Louisiana in 1985 and at Lake Griffin (28°50'N, 81°50'W), Lake Okeechobee (27°00'N, 81°00'W), Lake Woodruff NWR (29°05'N, 81°25'W), and Orange Lake (29°30'N, 82°10'W), Florida during 1987. Lacassine NWR (12,860 ha) is within the freshwater coastal marsh region of Louisiana and about one-half of the study site was a shallow (1-2 m) impoundment containing large stands of maidencane (Panicum hemitomon) and bulltongue (Sagittaria falcata) that supported dense nesting by alligators (an estimated 1 nest per 13 ha). Fruge (1974) provides a full synopsis of the area's vegetation. Descriptions of the Florida study areas are contained in Deitz and Hines (1980; Orange Lake), Jennings et al. (1987; Lake Griffin, Lake Woodruff NWR), and Millerson (1987; Lake Okeechobee).

Methods

The morphometric and reproductive variables recorded, their nearest unit of measure, and their abbreviations, are as follows: body mass (0.1 kg) = BM, clutch mass (g) = CM, clutch size = CS, dorsal cranial length (0.5 cm) [measured from the anterior snout to posterior supraoccipital] = DCL, snout-vent length (cm) = SVL, maximum tail girth (cm) = TG, total length (cm) = TOT. SVL measurements for crocodiles were taken from the snout tip to the anterior margin of the cloaca as per Australian convention (Webb and Messel, 1978), whereas data on alligators were recorded to the posterior cloaca consistent with the North American standard (Chabreck and Joanen, 1979). Morphometric measurements of alligators were from animals captured by short penetration harpoon (modified design of Webb and Messel, 1977a) or from individuals live-trapped at nest sites via an unbaited paddle trip snare (Mazzotti and Brandt, 1988).

Additionally, I examined reproductive tracts of female alligators harvested at Lacassine NWR in August-September 1985 to compare sizes of active breeding animals with those estimated from nest studies. Females were classified as sexually mature based on the color and texture of their ovaries (Graham, 1968; Joanen and McNease, 1980). Reproductive activity was assessed by the presence or absence of postovulatory ovarian follicles (Lance, 1989).

Nesting crocodiles were not captured, although their clutch parameters were recorded. Morphometric measurements were estimated as follows. Data from Cox (1985, Appendix 6) were supplemented to that of Hall and Johnson (1987) to derive a least squares relationship between CM and CS for nesting female *C. novaeguineae*. That equation (CM = -427.27 + 118.94 CS; $r^2 = 0.84$, $P < 0.001$, N = 40) was used to estimate CMs where unknown for individual clutches (N = 24). I also regressed CS against nesting female TOT (modified from Hall and Johnson, 1987) to estimate female TOTs for clutches where the adult was unobserved (N = 55), whereby TOT = 119.88 + 3.85 CS ($r^2 = 0.88$, $P < 0.001$, N = 9).

Estimated TOTs were then transformed to SVL estimates by using equation 2 of Montague (1984b): SVL = 5.73 + 0.49 TOT (r^2 = 0.95, N = 150).

The method for analysis of *C. novaeguineae* oviposition season data is described by Caughley (1977:72-78). The dates of nest detection were corrected to the dates of egg deposition through the use of embryo growth curves (Hall, 1985b).

Results

Alligator mississippiensis

The morphometric data on female alligators from Florida associated with known clutch data (N = 11) were too few to permit meaningful comparisons among study sites; however, regression slopes between areas were similar to each other and the data were thus pooled for analyses. Since among site resemblances were strong, equations derived from those data were also used to calculate snout-vent length (SVL) estimates of Florida and Louisiana animals for which only the clutch masses (CM) or clutch sizes (CS) were known. SVL was chosen as a more relevant indicator of adult female size than total length (TOT) due to the high proportion of tail injuries among crocodilians (Webb and Messel, 1977b, Montague, 1984a, Magnusson, 1985).

The best variable for predicting the size of an adult female alligator from a single attribute external to the animal was CH, although the dorsal cranial length (DCL) measurement of an isolated skull was a slightly more sensitive predictor of SVL (Table 4-1, Fig. 4-1). The relations between these and other tested factors were essentially isometric and were not significantly enhanced by the use of logarithmic transformations.

Allometric growth in skull length to body proportions within the Crocodylia has been documented (Kalin, 1933; Webb and Messel, 1978, Hall, 1985a), but this was not observed within the size range (97-140 cm SVL) of female alligators in this study. A trend toward allometry of DCL would probably be present in larger animals, but may be sex-specific and outside the body lengths attained by female alligators.

Where morphometric data on the associated females were lacking, I derived SVLs for nesting female alligators from Lake Woodruff NWR, Orange Lake, and Lacassine NWR from their CHs (equation 3, Table 1). Estimated sizes ($\bar{x}$ = 119.6 cm) did not differ (t = -6.37, N = 11, P > 0.05) for animals on which actual sizes ($\bar{x}$ = 119.5 cm) were obtained. Thus, estimates were pooled with captured nesting female data to develop demographic profiles of breeding females from these populations (Fig. 4-2).

Nesting alligators (pooled values of actual and estimated sizes) at Orange Lake ($\bar{x}$ SVL = 106.0 ± 7.39 SD, N = 4) were similar to, but slightly smaller than (t = 0.71, P

Table 4-1. Regression equations and standard error of the regression for predicting sizes of nesting female *Alligator mississippiensis* from single source attributes. BM = body mass (kg), CM = clutch mass (g), CS = clutch size, DCL = dorsal cranial length (cm), SVL = snout-vent length (cm), TG = tail girth (cm), TOT = total length (cm)

Equation No. & Predictor X		Estimated Value Y	Equation	SE	r^2	N	Sig. Level
1.	CM	BM	Y = 7.91 + 0.0125 X	10.07	0.54	11	P < 0.01
2.	CM	DCL	Y = 24.77 + 0.0021 X	1.14	0.73	11	P < 0.001
3.	CM	SVL	Y = 91.40 + 0.0085 X	4.60	0.72	11	P < 0.001
4.	CM	TG	Y = 31.23 + 0.0073 X	4.27	0.69	11	P < 0.001
5.	CM	TOT	Y = 181.65 + 0.0159 X	9.33	0.69	11	P < 0.002
6.	CS	BM	Y = -13.40 + 1.5185 X	10.66	0.56	13	P < 0.003
7.	CS	CM	Y = -1317.6 + 112.9 X	412.75	0.78	11	P < 0.001
8.	CS	DCL	Y = 21.01 + 0.2602 X	1.74	0.58	13	P < 0.002
9.	CS	SVL	Y = 72.98 + 1.1148 X	6.59	0.64	13	P < 0.001
10.	CS	TG	Y = 17.39 + 0.9230 X	4.60	0.72	13	P < 0.001
11.	CS	TOT	Y = 144.41 + 2.1512 X	12.87	0.64	13	P < 0.001
12.	DCL	SVL	Y = 0.045 + 3.7406 X	3.27	0.94	16	P < 0.001
13.	SVL	BM	Y = -121.37 + 1.4443 X	5.45	0.93	16	P < 0.001
14.	SVL	TOT	Y = -1.4975 + 1.9804 X	3.70	0.98	16	P < 0.001
15.	TG	BM	Y = -68.22 + 2.1633 X	6.84	0.89	16	P < 0.001

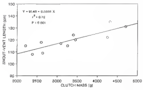

Figure 4-1 Regression plot of clutch mass and nesting female alligator snout-vent length.

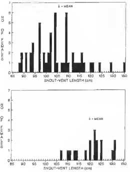

Figure 4-2. Size structures of nesting female *Alligator mississippiensis* from harvested (Orange Lake and Lacassine National Wildlife Refuge - top) and protected (Lake Woodruff National Wildlife Refuge - bottom) populations.

> 0.05), animals at Lacassine NWR ($\bar{x} = 110.1 \pm 8.89$, $N = 9$). Both samples were from populations exposed to regulated harvest. However, reproductive females at Orange Lake ($t = 3.01$) and Lacassine NWR ($t = 2.93$) were significantly smaller ($P < 0.01$) than alligators nesting at Lake Woodruff NWR ($\bar{x} = 120.1 \pm 7.49$, $N = 18$), which was a protected population. Furthermore, the sizes of nesting alligators from Lacassine NWR did not differ ($t = 1.43$, $P > 0.05$) from that of harvested females ($\bar{x} = 104.0 \pm 11.95$ SD, $N = 40$) who had nested that year, based on reproductive tract analysis. Thus, those size distributions were included in Figure 4-2. Although sample sizes from Orange Lake are small, those estimates are consistent with observations on the mean size of sexually mature female alligators removed from those systems during regulated harvest (A. Woodward, pers. comm.). The Lake Woodruff NWR sample encompassed about one third of the known nesting segment for that season so those estimates are probably not strongly biased.

I converted estimated SVL measurements for Louisiana alligators to TOT estimates by using equation 14 of Table 4-1 which was developed from Florida data. The same SVL values were then compared with transformed TOT estimates derived from Louisiana observations, whereby female SVL = $-2.24 + 0.5035$ TOT and body mass (BM) = $1.35 - 0.0378$ TOT + 0.0000046 TOT^3 (Chabreck and Joanen, 1979). These results indicated that female alligators from Louisiana possess longer TOTs than do Florida animals of an equivalent SVL; hence, with corresponding SVL, alligators from Louisiana had a heavier BM than Florida specimens. Consequently, the relative clutch mass (expressed as the ratio of ([(CM / 1000) / BM] x 100) was depressed in Louisiana females ($\bar{x}$ = 5.12 ± 0.41 SD, range = 4.7–5.8) when contrasted with Florida alligators ($\bar{x}$ = 6.82 ± 1.14, range = 5.1–8.7). This difference ($t = 4.01$, $P < 0.001$) might seem to be an artifact of the larger mean SVL (119 cm) of females composing the Florida sample. However, the comparable relative clutch mass for a Louisiana individual with an SVL of 121 cm was only 5.6, suggesting that the difference is real.

Crocodylus novaeguineae

The estimated mean SVL for 60 individuals (excluding four captives) was 104.1 cm ± 10.89 SD (Fig. 4-3). Estimated CM and BM (equation 83 of Montague, 1984b) for a crocodile of this size were 2,001 g and 38.2 kg, respectively. Relative clutch mass was 5.2, which lies within the interval of 4–7% previously reported for the species (Hall and Johnson, 1987).

The lower mean SVL of C. novaeguineae compared to alligators was a reflection of smaller adult size. Maximum recorded size (TOT) for female C. novaeguineae is 2.65 m

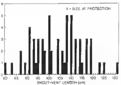

Figure 4-3 Size structure of nesting female *Crocodylus novaeguineae* in Lake Murray District, Papua New Guinea.

(Hall and Johnson, 1987), whereas female alligators can attain 2.87 m (Joanen and McNease, 1989).

The sizes (SVL) of nesting crocodiles reported here encompassed the minimum and maximum known range of reproduction by the species. Since data representing the upper, but not the lower, limit of the reproductive curve were available for alligators, I hypothesized that an estimate of the minimum size at reproduction in alligators would be proportional to the maximum adult female size ratio between these species (0.92). To test this assumption, I took the lowest observed SVL value for *C. novaeguineae* (80 cm), added 3 cm to make the measurement equivalent to that for alligators (see METHODS), and obtained a predicted SVL estimate of 90 cm (83 / 0.92) for alligators. This value closely approximated that observed (88 cm) for the smallest reproductively active female alligator that I found during reproductive tract analysis of harvested animals from Lacassine NWR and is similar to that for a 1.71 m TOT female observed during incubation (Joanen and McNease, 1989). Thus, in these two crocodilians, females appear capable of nesting once they have attained about 55-60% of maximum TOT.

Existing legislation designed to safeguard breeding population segments protects PNG crocodiles above 51 cm commercial belly width from harvest. This measurement is the equivalent of an animal with an SVL of 108 cm (209 cm TOT) (equation 12 of Montague, 1984b). However, based on the analysis presented here, 57% (95% confidence intervals = 40-73%) of nesting *C. novaeguineae* were below that size. A previous estimate of 74% (Hall and Johnson, 1987) was based on visual estimates of attendant nesting females. The discrepancy among these estimates is due to the clustering around the minimum size at protection (see Fig. 4-3). Elsewhere, Cox (1985) found that 86% of female *C. novaeguineae* from northern Papua New Guinea killed at their nest sites were below the size protected by law.

The nesting season for *C. novaeguineae* from Lake Murray is almost exclusively coincidental with the wet season (Hall, 1985b). Unlike American alligator populations that confine egg laying activities to a period of approximately three weeks during June or early July (Joanen and McNease, 1979), Lake Murray crocodiles oviposit during an interval more than ten times as long (Fig. 4-4). The mean oviposition date was February 6 ± 345 days SD, far in excess of a 30 day SD characteristic of populations that follow birth flow models (Dittus, 1981). Clutch size remained nearly constant throughout the oviposition period.

Discussion

This study clearly demonstrates that demographic interpretations of the nesting female segments of crocodilian populations are possible on the basis of associated clutch parameters. Although nesting densities

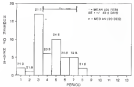

Figure 4-4. Nesting seasonality, adjusted to reflect oviposition dates, for wild New Guinea crocodiles (*Crocodylus novaeguineae*) from Lake Murray, Papua New Guinea. Mean clutch sizes indicated above period bars. Period dates: 1 = 23 Sep-20 Oct, 2 = 21 Oct-17 Nov; 3 = 18 Nov-15 Dec, 4 = 16 Dec-12 Jan; 5 = 13 Jan-09 Feb; 6 = 10 Feb-09 Mar; 7 = 10 Mar-06 Apr, 8 = 07 Apr-04 May; 9 = 05 May-01 Jun, 10 = 02 Jun-29 Jun; 11 = 30 Jun-27 Jul; 12 = 28 Jul-24 Aug; 13 = 25 Aug-22 Sep.

have been used as an index of crocodilian populations (McNease and Joanen, 1978; Hollands, 1987), monitoring of the reproductive cohorts per se has not been possible until now due to the paucity of data on breeding females associated with specific nests. The methods I used circumvented that difficulty and permitted a reliably accurate determination of the size of nesting females among populations from existing data sets composed of CM or CS sions. These results indicate that CM is a better predictor of adult female size than CS for both alligators and crocodiles. They lend further support to the use of SVL measurement as the most biologically meaningful criterion of crocodilian size since female alligators with equivalent SVLs from geographically disjunct populations are not equivalent in TOTs. This phenomenon was also reported for *Crocodylus porosus* in which Bornean crocodiles possessed longer tails than did Australian animals (Webb and Messel, 1978).

Temperate alligators and tropical crocodiles share similar behavioral repertoires (Garrick and Lang, 1977). However, the timing and duration of reproductive seasonality differs strongly among *A. mississippiensis* and southern-form *C. novaeguineae*.

The full complement of reproductive activities (courtship through hatching) occurs between mid-March and mid-September in *A. mississippiensis* (Ferguson, 1985), whereas reproduction in *C. novaeguineae* is circa-annual (Hall and Johnson, 1987). In addition, subsets of the reproductive cycle are temporally compressed in alligators--incubation requires 9-10 weeks to completion (Joanen, 1969) versus 12-13 weeks for New Guinea crocodiles (Hall and Johnson, 1987). Consequently, the genitalia of hatchling alligators are morphologically undifferentiated compared to hatchling crocodiles. Thus, neonate alligators cannot be reliably sexed by cloacal examination (Joanen and McNease, 1978), although gender determination of hatchling crocodiles by that method is possible (Webb et al., 1984). Clearly, the narrow time interval for egg laying within alligator populations characterizes the species as having a pulse reproductive mode (Caughley, 1977), contrasted with the flow model of *C. novaeguineae*. Why these species differ in this respect, and what some of the probable consequences of each mode on population recruitment are, remain to be answered.

The timing of oviposition by American alligators is negatively correlated with ambient temperatures during the spring months of March to May ($P < 0.01$; i.e., years of colder mean spring temperatures result in later mean dates of egg laying). Egg deposition also coincides with the maximal photoperiod interval. Although rainfall does not effect the time of nesting it does influence the degree of nesting (Joanen and McNease, 1979; Kushlan and Jacobsen, 1990). This agrees with what one should expect of a poikilothermic species in temperate habitat where marked seasonal fluctuations in incident sunlight and temperature greatly constrict the period of primary and secondary productivity compared to tropical environments. It is also not surprising that alligators have a size-specific dominance breeding hierarchy whereby larger males and females copulate earlier and more frequently within a season than do smaller conspecifics (Ferguson, 1985; Vliet, 1987), given the limited temporal framework within which mating must occur (two months annually). Accordingly, model simulations for alligator populations are largely deterministic since the proximate factors effecting recruitment are essentially stable and predictable, whereas stochastic events (such as hurricanes) are relatively rare (Nichols et al. 1976). However, the impact of stochasticity on alligator populations can be devastating. For instance, the early arrival of 1985 hurricanes in Louisiana resulted in the loss of about 80-90% of the coastal alligator egg crop due to flooding (T. Joanen, pers. comm.). The long-term effects of such occurrences on the population are undoubtedly lessened because the potential longevity of alligators (and other crocodilians) may exceed 50 years (Chabreck and Joanen, 1979, Graham, 1968). Thus, breeding segments of crocodilian populations may be composed of 20 or more active age cohorts. Some female crocodilians, though, eventually become reproductively senescent (Graham, 1968;

Joanen and McNease, 1980). For further discussion on the consequences of "one-year wipeouts", see comments by Abercrombie (1989).

In contrast, the proximate factor apparently governing the reproductive cycle of *C. novaeguineae* is annual precipitation, as photoperiod and temperature are fairly uniform throughout the year. Pronounced variation in rainfall occurs both within and among years, with most of the variance accounted for by patterns of dry season precipitation (Hall, CHAPTER 3). Although the reproductive hormonal cycle has yet to be studied in this species, courtship behavior appears to be synchronous with the onset of the wet season rains as egg deposition spans the duration of the wet season. Crocodiles seem to cue on the high water mark of the previous year as their nests are constructed on land above that point or are built on mounds of floating herbaceous vegetation that rise and fall with water levels (Hall and Johnson, 1987). The prolonged seasonality of nesting makes it unlikely that catastrophic stochastic events (e.g., earthquakes, fires, storms) will eliminate an entire cohort as can happen in alligator populations (above). Whether or not a size-specific dominance breeding hierarchy exists in wild *C. novaeguineae* is also unknown, although such behavior is exhibited by captive animals (Lang, pers. comm.; Hall, pers. obs.). I suspect that if that behavior occurs in the wild, the intensity of interactions should be relaxed compared to alligators since the interval in which spermatogenesis and vitellogenesis can occur is potentially four times as long in *C. novaeguineae*.

Although techniques for aging crocodilians and other long-lived reptiles have been developed (Graham, 1968; Hutton, 1986; Zug et al., 1986; Zug and Rand, 1987), they produce estimates that suffer from low precision and accuracy for all but very young cohorts. It is partly for this reason that Nichols (1987) argued for the use of size, rather than age-specific, cohort analysis of crocodilian populations. In addition, a population with a flow mode of reproduction like southern-form *C. novaeguineae* would further obfuscate such interpretations, especially if making inter-population comparisons with northern-form *C. novaeguineae* which has a much shortened reproductive season (Cox, 1985). Since reproductive mode may differ among populations within a species, these generalizations should not be assumed to uniformly apply to other crocodilians on the basis of latitudinal gradients.

I believe that the effects of controlled harvests may have operated differentially on the breeding female segments of these populations of *A. mississippiensis* and *C. novaeguineae*. The similarity of mean sizes of nesting female alligators in populations exposed to harvest (Lacassine NWR and Orange Lake) and the significantly larger mean size of animals nesting in an unhunted population (Lake

Woodruff NWR) suggests: (1) the existence of a reservoir of sexually mature, but socially subordinate, animals in recovered, protected alligator populations; (2) that such animals fail to nest because they are exploitatively or behaviorally inferior to larger, dominant females; and, (3) that they will not achieve active reproductive status until either attaining larger size or until a socially mature female is removed through natural mortality or managed harvest, thus producing a reproductive vacancy. The mean size of nesting females in the protected population was 14% longer, but 72% heavier, than that of females in harvested populations. Thus, even relatively small differences in length can place smaller sexually mature females at a great competitive disadvantage with larger conspecifics.

A caveat of the preceding paragraph is the implicit assumption that competition among females is occurring due to some strongly limiting factor, presumably access to nesting habitat. Habitat quality differs greatly throughout the range of these species, where nesting densities are generally low in riverine areas, intermediate in lake habitats, and highest in grassland marshes. Among the latter, *Panicum hemitomon* marsh is considered qualitatively inferior to coastal brackish and intermediate marshes in Louisiana (T. Joanen, pers. comm.). Nesting habitat appears not to be a limiting factor in these marshes and they support the highest nesting density of alligators in the

United States. The percent of annual nesting by adult female alligators in these marshes is over twice as high (68%, Joanen and McNease, 1980) as reported in Florida (28%, Kushlan and Jacobsen, 1990) or South Carolina (27.5%, Wilkinson, 1984). Accordingly, management harvest quotas in Louisiana are based on habitat type (Joanen and McNease, 1987).

These results also suggest that selective culling of larger nesting female alligators may lead to accelerated population growth through the creation of higher nesting densities and incremented egg and hatchling production (see Hines and Abercrombie, 1987 and Abercrombie, 1989). Clutch size increases with female size in A. mississippiensis (Ferguson, 1985) and C. novaeguineae (Hall and Johnson, 1987). A decrease in mean clutch size resulting from the prudent removal of large nesting female alligators should be offset by an increase of smaller females that nest in the absence of more dominant females.

The relatively short, clearly demarcated nesting season of alligators (in addition to differential seasonal habitat use by adult males and females) favors management practices that selectively cull adult animals following the completion of reproduction. Such measures would not be feasible for the management of southern-form C. novaeguineae due to its very extended reproductive period. Harvest regulations target alligators larger than 1.2 m TOT, whereas harvests of crocodiles are restricted to animals less than 2.1 m. Although the life history traits of crocodilian species generally support the removal of juvenile and subadult size classes (Messel et. al, 1981; Magnusson, 1986), most reproductively active C. novaeguineae were nesting at sizes smaller than that protected by law and were thus also exposed to harvest. Consequently, the estimated annual turnover in the female breeding segment was high (> 60%) and population growth retarded (Hall and Johnson, 1987).

Additional studies of this nature are needed to more fully evaluate whether or not site-specific differences exist among slopes for the regression models presented herein and to assess their predictive ability for constructing demographic profiles of breeding female crocodilian populations. Although based on small sample sizes, these models are practical because they provide a fair to excellent accounting of the associated variances (r^2 values) for each model. Preliminary tests indicate that they provide excellent agreement of estimated with actual sizes of nesting female alligators subsequently captured (H. F. Percival, unpubl. data). The use of multiple regression analysis did not enhance these values since predictors were highly correlated with each other.

In conclusion, accurate and precise estimates of nesting adult female crocodilians are feasible in the course of activities normally conducted by ecologists and management authorities, with little expenditure and justifiable effort. This has proven effective with both hole nesting *Crocodylus acutus* (Mazzotti and Brandt, 1988) and mound nesting species (this study). Data of these type, hitherto rarely obtained, are of demonstrable value to biologists and agency personnel concerned with crocodilian conservation. An initial understanding of the sizes of reproductive females provides a mechanism for the long-term monitoring of crocodilian populations in response to protection or induced harvest strategies, as well as affording a practical manner in which unanswered questions pertaining to the reproductive longevity and success of individual animals may be addressed.

CHAPTER 5

CRANIAL MORPHOMETRY OF NEW GUINEA CROCODILES (*Crocodylus novaeguineae*): ONTOGENETIC VARIATION IN RELATIVE GROWTH OF THE SKULL AND AN ASSESSMENT OF ITS UTILITY AS A PREDICTOR OF THE SEX AND SIZE OF INDIVIDUALS

Introduction

Papua New Guinea (PNG; Fig. 5-1) harbors two species of sympatrically distributed crocodilians: the New Guinea crocodile (*Crocodylus novaeguineae*), endemic to the main island of New Guinea, and the wide-ranging saltwater crocodile (*C. porosus*). Both species are commodities of great economic value as hides and meat, and much effort has been made to improve the biological and economic return of these natural resources (Bolton, 1980, 1981). Trade in live crocodilians or their byproducts is regulated by the Convention on International Trade of Endangered Species of Fauna and Flora (CITES) (King, 1973) since all 23 species of the order Crocodylia (alligators, caimans, crocodiles, gharial, and tomistoma) are classified as threatened or endangered with extinction (Honegger, 1979; Groombridge, 1982). The more abundant species in PNG is *C. novaeguineae* and it comprises 75-80% of the annual export (> 98% of study area exports) of crocodile hides (Anon., 1981; Whitaker,

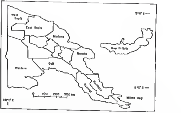

Figure 5-1. Map of Papua New Guinea indicating provinces of crocodile harvest, excluding Manus (2°0'S, 147°0'E), New Ireland (3°0'S, 151°30'E) and the North Solomons (6°0'S, 155°0'E). Right border of map is 153°E.

1980; Whitaker and Kemp, 1981; Hall, CHAPTERS 2 and 3). Due to the comparative abundance of this species and the limited availability of *C. porosus* material, I chose *C. novaeguineae* for this study.

Harvest data of PNG crocodiles provide an indirect measure of size (commercial belly width; see METHODS), but no information on the sex or age of individuals. Gathering data from freshly killed specimens is not feasible due to rapid deterioration of hides and logistic constraints (remote areas, manpower, and economics) These facts necessitate funding of long-term studies to generate adequate data on caught wild individuals to monitor growth rates and population sex ratios. Such costs have been prohibitive to all but a few external research agencies. In addition, crocodilians are extremely wary animals that develop rapid learning avoidance to capture (Bustard, 1968)

Consequently, I sought to develop a cost-effective, alternative method to address these problems through morphometric sampling of discarded crocodilian skulls from hunter harvests as a practical management tool to aid in monitoring resource use. The objectives of this study were to: (1) examine and quantify ontogenetic patterns in relative growth of the skull in a crocodilian, *Crocodylus novaeguineae*, and (2) assess the utility of the functional patterns of relative growth as a predictor of gender. Such knowledge will permit determination of population structural parameters of future harvests. Thus, demographic trends may be monitored and the potential to manage the resource enhanced.

Background

Growth in the Order Crocodylia is thought to be indeterminate (Cott, 1961; Jacobsen and Kushlan, 1989; Griebin, 1990). Crocodilians exhibit typical size dimorphism, whereby males grow longer and heavier than females (Neill, 1971). However, this discrepancy may not be apparent where regulated crocodilian harvests occur if the upper size limit is below the point where the divergence between sexes is pronounced (such as in New Guinea). Other than size, sexual dimorphism in crocodilians is evident only in socially mature, adult male gharials (Gavialis gangeticus) that exhibit a secondary bulbous snout protuberance (Nasu, 1980). However, the reliability of this character remains uncertain as a necropsied adult possessing such a feature was found to be female (Martin and Bellairs, 1977). Thus, to date, manual probing of the cloaca (Chabreck, 1963) or vivisection (Magnusson and Hero, 1990) are the only certain means of determining gender in a living individual, except where size dimorphism is apparent.

As a group, crocodilians are long-lived (40+ years) vertebrates and dimorphic attributes of growth appear to initiate in early life by age five (Webb et al., 1978, Chabreck and Joanen, 1979). The disparity of such growth is strongly influenced by incubation temperatures during embryogenesis (Ferguson and Joanen, 1983; Webb and Smith, 1984). Functional changes in the rates and directions of growth for areas of the crocodilian skull are also known to occur with the age and size of individuals (Dodson, 1975).

In light of the foregoing, I hypothesized that the skulls of crocodilians (beyond the early age classes) should also exhibit a dimorphic suite of characters to accompany the ontogenetic changes in growth of body size with respect to sex. In essence, the skull of a female crocodile compared to that of an equal length male of age X will belong to an animal of age X+t. Thus, the shifts in ontogenetic patterns of relative growth of the skull of comparable size individuals should be more pronounced in females than males of equivalent size, and become even more disparate as size/age increases. As such, the gender of like-size individual skulls is indiscernible with specimens in hand (Fig. 5-2), but may become apparent when patterns of growth are viewed and analyzed in a multidimensional framework.

The quantitative study of growth in crocodilians is fairly new. Early descriptive investigations on aspects on embryonic growth include those by Parker (1883), Clarke (1891), Voeltzkow (1902), Reese (1908), McIlhenny (1934, 1935), and Deraniyagala (1939). More recent studies on this

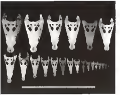

Figure 5-2. Ontogenetic series of *Crocodylus novaeguineae* skulls. Specimens are Louisiana State University Museum of Zoology (LSUMZ) series unless indicated otherwise. Top row (l-r): LSUMZ 44741, 44742, 44740, 44739, 44736, 44738. Bottom row (l-r): LSUMZ 44735, 44734, FMH0152 (author's collection), LSUMZ 44733, 44732, 44731, 44730, 44729, 44728, 44727, 44726, 44725, 44724, 44723, 44722, 44721.

subject include Magnusson and Taylor (1980), Bolton (1981), Vásquez Ruesta (1982-83), Webb et al. (1983b), Ferguson (1985), Hall (1985b), and Deeming and Ferguson (1990). Growth of posthatching animals has been investigated by several authors. Kramer and Medem (1955) reviewed proportional gross morphology of extant crocodilians as did Wermuth (1964). Other reports on aspects of gross morphological growth focused on a few individual species These include: *Alligator mississippiensis* (McIlhenny, 1934; Dodson, 1975; Nichols et al., 1976; Chabreck and Joanen, 1979; Jacobsen and Kushlan, 1989; Brisbin, 1990), *Caiman crocodilus* (Staton and Dixon, 1975; Gorzula, 1978; Ayarzaguena, 1984, Ouboter and Nanhoe, 1989; Thorbjarnarson, 1990), *Crocodylus niloticus* (Cott, 1961; Graham, 1968, 1976; Hutton, 1987a and b), *C. novaeguineae* (Lawson, 1972; Montague, 1982; Jelden, 1984), *C. porosus* (Banks, 1930; Webb, 1977; Webb and Messel, 1978; Webb et al., 1978), *Crocodylus siamensis* (Muller, 1923, 1927), and *Paleosuchus trigonatus* (Magnusson and Lima, in press). The works of Parker (1882), Mook (1921a and b), Kalin (1933), Iordansky (1973), Langston (1973), and Greer (1974) were confined to cranial growth in crocodilians. However, the quantitative relationships between size, sex, and age of most crocodilian species remain unknown.

General ontogenetic trends of crocodilian cranial growth have been reported by Mook (1921b), Kalin (1936, 1955), Brongersma (1941), and Iordansky (1973). However, these authors made no quantitative assessment of growth with size, sex, or age. Dodson (1975) later presented allometric coefficients for 27 attributes of cranial growth for *A. mississippiensis*, irrespective of sex or age. Subsequently, Webb et al. (1974) reported the interorbital width to be a sexually dimorphic character in Australian *C. porosus*. However, the predictive values of their discriminant models to correctly identify gender were low except for larger animals; an evident reflection of size dimorphism. Similarly, Montague (1984b) reported sexual dimorphism in the midpoint width of the cranial roof in *C. novaeguineae*, but concluded that this trait was an unreliable indicator of sex.

Study Area and Methods

Morphometry

Morphometric measurements of 425 *C. novaeguineae* (342 skulls and 83 live specimens) were recorded during 1980-1982. These include 162 males and 83 females plus 180 individuals of unknown gender. All animals were referable to the southern form of this species (Hall, 1989). Most specimens were collected in Lake Murray District, Western Province, PNG (Fig. 5-3), while a handful came from Central Province (Brown River, Waigani Swamp), PNG. Lake Murray District is primarily tropical moist forest with pronounced

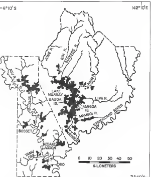

Figure 5-1. Middle Fly (left) and Lake Murray (right) subdistricts in the Lake Murray District, Western Province, Papua New Guinea.

wet (November-May) and dry (June-October) seasons. Annual mean precipitation is 306 cm and 325 cm in Balboa and Pangoa, respectively, in the Lake Murray subdistrict and 258 cm at Bosset in the Middle Fly subdistrict (Hall, CHAPTER 3). Detailed descriptions of the study area are presented elsewhere (Hall, 1983; Hall and Johnson, 1987).

I obtained data from skulls provided by hunters and from culled captive stock caught from the wild. Additionally, I examined two skulls from Western Province at the British Museum (Natural History), London. All skulls were dried at ambient air temperature for at least 30 days prior to inspection. Pre- and post-drying measurements were made on culled captive animals to estimate shrinkage of certain characters. Thus, correction factors can be applied to data that I also obtained from live individuals or from preserved, but uncleaned skulls.

The morphometric measurements taken (Figs. 5-4 - 5-8), their abbreviations, explanation, and the nearest whole unit of value employed are listed in Table 5-1. Measurements up to 150 mm were taken with 0.05 mm dial calipers. A steel tape was used for larger dimensions. Body mass was weighed on a Salter clock scale. Manual probing of the cloaca (Chabreck, 1963) was used to determine sex.

Ratio indices were used for skull characters to reflect relative growth. The indices used and their methods of calculation are indicated in Table 5-2. Cranial indices

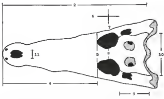

Figure 5-4. Dorsal view of Crocodylus novaeguineae cranium showing measurements taken. 2 = DCL, 3 = CW, 4 = SL, 5 = SW, 6 = OL, 7 = OW, 8 = IOW, 9 = LCR, 10 = WCR, 11 = WN. See METHODS for explanation.

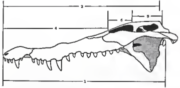

Figure 5-5. Lateral view of Crocodylus novaeguineae cranium showing measurements taken. 1 = CL, 2 = DCL, 4 = SL, 6 = OL, 9 = LCR. See METHODS for explanation.

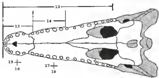

Figure 5-6. Palatal view of *Crocodylus novaeguineae* cranium showing measurements taken. 12 = UM, 13 = PXS, 14 = MXS, 15 = PM4L, 16 = PM4W, 17 = M5L, 18 = M5W.

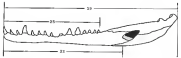

Figure 5-7. Lateral view of *Crocodylus novaeguineae* mandible showing measurements taken. 19 = ML, 22 = DL, 25 = LM. See METHODS for explanation.

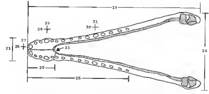

Figure 5-8. Dorsal view of *Crocodylus novaeguineae* mandibles showing measurements taken. 19 = ML, 20 = LMS, 21 = WMS, 23 = DW, 24 = WSR, 25 = LM, 26 = D1L, 27 = D1W, 28 = D4L, 29 = D4W, 30 = D11L, 31 = D11W. See METHODS for explanation.

Table 5-1. Morphometric and miscellaneous variables recorded on Crocodylus novaeguineae indicating their abbreviations, explanation, and the nearest whole unit of measurement. For bilateral categories, growth was assessed unilaterally from the right side, except where damaged.

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(1) CL (cranial length). Anterior tip of snout to posterior surface of occipital condyle. 1 mm.

(2) DCL (dorsal cranial length). Anterior tip of snout to posterior tip of supraoccipital (medial posterior margin of cranial roof). 1 mm.

(3) CW (cranial width). Distance between the lateral surfaces of the mandibular condyles of the quadrates. 1 mm.

(4) SL (snout length). Anterior tip of snout to anterior orbital border, measured diagonally. 1 mm.

(5) SW (basal snout width). Width across anterior orbital borders. 1 mm.

(6) OL (maximal orbital length). 1 mm.

(7) OW (maximal orbital width). 1 mm.

(8) IOW (minimal interorbital width). 1 mm.

(9) LCR (length of the postorbital cranial roof). Distance from the posterior orbital border to the posterolateral margin of the squamosal. 1 mm.

(10) WCR (posterior width of the cranial roof). Distance between the posterolateral corners of the squamosals. 1 mm.

(11) WN (maximal width of external nares). 1 mm.

(12) PXS (length of palatal premaxillary symphysis). 0.05 mm.

(13) MXS (length of palatal maxillary symphysis). 0.05 mm.

(14) UM (length of upper ramus). Anterior tip of snout to posterior margin of distal most maxillary alveolus. 1 mm.

Table 5-1 (cont.).

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(15) PM4L (maximal length of fourth [largest] premaxillary alveolus). 0.05 mm.

(16) PM4W (maximal width of fourth premaxillary alveolus) 0.05 mm.

(17) M5L (maximal length of fifth [largest] maxillary alveolus). 0.05 mm.

(18) M5W (maximal width of fifth maxillary alveolus). 0.05 mm.

(19) ML (mandible length). Anterior tip of dentary to the posterior tip of the retroarticular process. 1 mm.

(20) LMS (length of the mandibular symphysis). 1 mm.

(21) WMS (maximal width across the mandibular symphysis). 1 mm.

(22) DL (dentary length). Anterior tip of dentary to the anterior external mandibular fenestra. 1 mm.

(23) DW (dentary width). Lateral interalveolar width of dentary at the posterior margin of the mandibular symphysis. 1 mm.

(24) WSR (surangular width). Posterolateral width across surangulars at point of jaw articulation. 1 mm.

(25) LM (length of lower ramus). Anterior tip of dentary to posterior margin of distal most dentary alveolus. 1 mm.

(26) D1L (maximal length of first [third largest] dentary alveolus). 0.05 mm.

(27) D1W (maximal width of first dentary alveolus). 0.05 mm.

(28) D4L (maximal length of fourth [second largest] dentary alveolus). 0.05 mm.

(29) D4W (maximal width of fourth dentary alveolus). 0.05 mm.

Table 5-1 (cont.)

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(30) D11L (maximal length of eleventh [largest] dentary alveolus). 0.05 mm.

(31) D11W (maximal width of eleventh dentary alveolus) 0.05 mm.

Other measurements and data recorded, where known, were:

(32) SVL (snout-vent length). Anterior tip of snout to anterior cloaca. 1 cm.

(33) TTL (total length). 1 cm.

(34) BW (commercial belly width). The width across the ventral and lateral scales between the distal margins of the third transverse row of dorsal scutes (Fig. 5-9). 1 cm.

(35) BM (body mass). 0.1 kg.

(36) Sex.

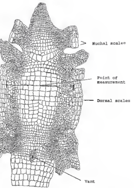

Figure 5-9. Illustration of crocodile belly skin (modified from Parker, 1981). Commercial belly skins in Papua New Guinea are measured between the distal margins of the third row of keeled dorsal scales. To be legal, a skin must not exceed 50.8 cm (20") belly width and must also include at least two rows of keeled dorsal scales on either side. In 1981 a minimum size restriction of 17.8 cm (7") commercial belly width was imposed.

Table 5-2. Relative growth indices used for skull variables of Crocodylus novaeguineae indicating abbreviations and methods of calculation

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(1) RCW (relative cranial width) = cranial width / dorsal cranial length [CW / DCL].

(2) RLST (relative length of snout) = snout length / dorsal cranial length (SL / DCL).

(3) RWST (relative width of snout) = basal width of snout / snout length [SW / SL].

(4) ROL (relative orbital length) = maximal orbital length / dorsal cranial length [OL / DCL].

(5) ROW (relative orbital width) = maximal orbital width / maximal orbital length [OW / OL].

(6) RWI (relative interorbital width) = minimal interorbital width / maximal orbital length [IOW / OL].

(7) RLR (relative length of postorbital cranial roof) = length of postorbital cranial roof / posterior width of cranial roof [LCR / WCR].

(8) RWN (relative width of external nares) = maximal width of external nares / dorsal cranial length minus snout length [OL / (DCL - SL)].

(9) RPXS (relative length of premaxillary symphysis) = length of premaxillary symphysis / dorsal cranial length [PXS / DCL].

(10) RMXS (relative length of maxillary symphysis) = length of maxillary symphysis / dorsal cranial length [MXS / DCL].

(11) RLUMR (relative length of upper ramus) = upper ramus length / dorsal cranial length [UM / DCL].

(12) RLSS (relative length of mandibular symphysis) = maximal length of mandibular symphysis / mandible length [LMS / ML].

(13) RWSS (relative width of mandibular symphysis) = maximal width across mandibular symphysis / maximal length of mandibular symphysis [WMS / LMS].

Table 5-2 (cont.).

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(14) RLD (relative length of dentary) = dentary length / mandible length [DL / ML].

(15) RWD (relative width of dentary) = dentary width / dentary length [DW / DL].

(16) RWM (relative width of mandible) = maximal width across surangulars at jaw articulation / mandible length [WSR / ML].

(17) RLLMR (relative length of lower ramus) = lower ramus length / mandible length [LM / ML].

For each of the five alveoli measured (PM4, M5, D1, D4, D11) the following ratios were used:

(18) RL (relative length of alveolus) = maximal alveolus length / dorsal cranial length (for upper alveoli [PM4 / DCL, M5 / DCL]) *or* mandible length (for lower alveoli [D1 / ML; D4 / ML; D11 / ML]).

(19) RW (relative width of alveolus) = maximal alveolus width / maximal alveolus length (e.g., M5W / M5L)

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used in this study were modified from Iordansky (1973) by substituting dorsal cranial length (DCL) for cranial length (CL) as an index divisor. The latter measurement includes the occipital condyle which is often broken during collection. Also, the former measurement is preferable since it can be recorded from living individuals, whereas the latter cannot. Mandibular indices were of my own design.

Voucher specimens that were imported to the United States were exported from PNG under the following CITES permit numbers: #10057-#10059, and #10296-#10299.

Analyses

Linear regression analysis was used to derive equations for the estimation of DCL from body size measurements or other skull attributes used as independent variables. Slopes and intercepts of regression formulae were compared by F-tests to evaluate for gender specificity. Coefficients were also calculated for the prediction of body size attributes from DCL by the same method.

Growth estimates for male C. novaeguineae to age nine and females to age 13 (Hall, CHAPTER 3) were fitted to a reparameterized Richards curve (Brisbin et al., 1986) of the form: $W_t = [A^{(1-m)} - (A^{(1-m)} - W_0^{(1-m)})\exp(-2t/T(m+1))]^{1/(1-m)}$ where the parameters are as follows. W_t and W_0 represent known body mass or length at time t and at time t=0 (hatching), A is the final asymptotic length or mass, while T and m represent the length of the total growing period and the Richards curve shape parameter, respectively. In this study W_t is 335 cm for males and 265 cm for females (below), while A is 28 cm for both sexes (Hall, 1985b). A second pair of models was constructed with respective W_t values of 360 and 285 (see RESULTS). The parameter T was estimated at 50 years for males and females and m was set at a value 0.667 after Brisbin (1990). A third pair of models using another Richards derivation, the Brody curve (Gates and Dohm, 1989) where the shape parameter m is 0, was calculated for comparative purposes using the first set of W_t values. This curve takes the form: $W_t = A[1-B\exp^{C(age)}]$, where W_t and A are as above, and B and C are constants with values of 0.9 and −0.2 in the models presented.

Gender analysis of relative growth ratios for C. novaeguineae was tested by two methodologies to assess the comparative robustness of each approach and their utility for properly classifying observations. A traditional parametric multivariate method, discriminant analysis (DISCRIM; SAS, 1988), was first used followed by a non-parametric binary classification tree analysis program (CART [California Statistical Software, Inc.]; Breiman et al., 1984). The CART methodology offers several important advantages over discriminant analysis in that it treats observations with missing values and that it states the decision rules by which classification trees are made.

Both DISCRIM and CART evaluate classification criteria by their performance in the classification of future observations. Initial error count estimates for each method were derived by summing the number of misclassified ear observations from the test data sets and dividing by the total number of observations. The resulting error rates are optimistically biased and referred to as 'apparent' error rates (AERs). To evaluate the correctness of these classification rates, crossvalidation data sets were created then analyzed for each method to reduce model biases and associated variances and to establish 'true' error rates (TERs). Crossvalidation is a form of jacknifing that treats n-1 out of n training observations as a learning set; it derives discriminant functions based on these n-1 observations and applies them to classify the one observation left out. Iterations are then performed successively for each of the remaining n training observations and a misclassification rate is calculated as above.

I further analyzed DISCRIM predictor models by using stepwise discriminant analysis (STEPDISC; SAS, 1988). This procedure selects a subset of variables from the original data set to provide a 'best fit' model for discrimination. Similarly, I then used the character variables selected by

CART in the initial analysis above to create a new series of comparative 'best fit' models for gender classification.

Results

General Morphology

Linear regression coefficients of body size and skull attributes used as independent variables to predict dorsal cranial length (DCL) are listed in Table 5-3. Most variables showed a slight allometry with increasing dorsal cranial length (Fig. 5-10). Allometry was most pronounced with respect to body mass (BM; Fig. 5-10d) for which logarithmic transformation ($\log_{10}$) was made. Several cranial (snout length [SL - Fig. 5-10g], cranial length [CL - Fig. 5-10e], upper ramus length [UL - Fig. 5-10q]) and mandibular measurements (mandible length [ML - Fig. 5-10v], dentary length [DL - Fig. 5-10y], lower ramus length [LM - Fig. 5-10ab]) exhibited near perfect ($r^2 > 0.99$) isometry as predictors of DCL. Correlations of body size and skull measurements with DCL were uniformly high, often extremely so. The fit of regression coefficients (r^2 values) was consistently better for males than females. Variability was most pronounced with respect to interorbital width (IOW) and dental alveoli.

Table 5-3. Linear regression coefficients for predicting dorsal cranial length (DCL) of *Crocodylus novaeguineae* from body size and other skull parameters by the equation Y = A + BX. where A is the Y intercept. B the slope. Equations are expressed separately by gender (M = males. F = females) where they differed by sex (P < 0.05), and are combined (M+F) where no such differences were detected. U = sex unknown. TOT = total sample. E = standard error of the regression model. r^2 = coefficient of determination, N = sample size.

Eqn No.	Predictor X	Sex	A	B	E	r^2	N
1	Snout-vent length[A] (SVL)	M	24.61	2.35	6.46	0.9603	126
2		F	24.37	2.39	6.38	0.9004	70
3		U	-0.73	3.22	3.09	0.9286	27
4		TOT	12.43	2.52	6.70	0.9866	223
5	Total length (TTL)[A]	M	13.97	1.25	6.44	0.9605	126
6		F	9.94	1.31	8.28	0.8726	72
7		U	0.84	1.48	1.52	0.9826	27
8		TOT	7.77	1.30	7.08	0.9852	225
9	Belly width (BW)[A]	M+F	95.41	3.09	11.29	0.8117	206
10		U	22.11	6.09	10.73	0.9832	12
11		TOT	78.91	3.56	13.90	0.8280	218
12	LOG_{10} Body mass (BM)[B]	M+F	2.04	0.25	0.01	0.8068	189
13		U	2.28	0.52	0.04	0.9141	6
14		TOT	2.00	0.29	0.02	0.9763	195

[A] Cm.

[B] Kg: following in mm.

Table 5-3 (cont.)

Eqn No.	Predictor X	Sex	A	B	E	r^2	N
15	Cranial length (CL)	M	1.55	0.93	2.93	0.9982	151
16		F	-5.02	0.96	2.24	0.9637	75
17		U	2.63	0.93	3.37	0.9976	89
18		TOT	1.92	0.93	3.04	0.9976	315
19	Cranial width (CW)	M	47.67	1.60	7.78	0.9875	151
20		F	19.68	1.94	5.66	0.9507	75
21		U	33.27	1.79	10.02	0.9786	89
22		TOT	44.20	1.66	9.24	0.9777	315
23	Snout length (SL)	M+F	21.40	1.37	2.62	0.9982	229
24		U	19.44	1.37	3.32	0.9982	94
25		TOT	20.69	1.37	3.03	0.9980	323
26	Snout width (SW)	M	54.81	2.20	8.82	0.9849	153
27		F	37.75	2.53	8.23	0.9281	76
28		U	29.01	2.69	13.27	0.9708	94
29		TOT	48.30	2.33	12.54	0.9648	323
30	Orbital length (OL)	M+F	-94.24	8.86	8.58	0.9792	226
31		U	-61.32	8.13	11.14	0.9794	94
32		TOT	-78.24	8.47	10.42	0.9745	320
33	Orbital width (OW)	M	-135.92	12.63	15.76	0.9461	150
34		F	-135.04	12.82	15.86	0.6161	75
35		U	-86.04	11.64	17.40	0.9499	94
36		TOT	-102.00	11.70	19.14	0.9113	319

Table 5-3 (cont.)

Eqn. No.	Predictor X	Sex	A	B	E	r^2	N
37	Interorbital width (IOW)	M	77.59	8.22	10.97	0.9756	152
38		F	75.15	8.70	11.59	0.8575	78
39		U	83.14	9.57	18.62	0.9426	94
40		TOT	74.17	8.60	14.82	0.9495	322
41	Length of cranial roof (LCR)	M+F	26.42	4.10	8.39	0.9817	229
42		U	-8.30	4.91	9.57	0.9848	93
43		TOT	15.44	4.35	10.38	0.9758	322
44	Width of cranial roof (WCR)	M	27.38	2.83	8.72	0.9852	153
45		F	23.37	2.96	8.23	0.9281	78
46		U	-0.008	3.37	10.95	0.9801	93
47		TOT	20.32	2.98	11.15	0.9721	322
48	Width of external nares (WN)	M	47.87	11.81	12.83	0.9681	153
49		F	47.85	12.14	11.77	0.8532	76
50		U	20.41	14.91	13.77	0.9843	90
51		TOT	43.99	12.40	15.67	0.9420	319
52	Length of premaxillary symphysis (PXS)	M	15.85	4.20	10.38	0.9775	125
53		F	44.00	3.83	7.78	0.9075	75
54		U	20.94	4.04	11.90	0.9732	82
55		TOT	21.52	4.08	10.42	0.9711	282
56	Length of maxillary symphysis (MXS)	M+F	19.89	4.70	17.01	0.9121	200
57		U	13.48	4.88	18.85	0.9331	83
58		TOT	17.66	4.76	17.39	0.9193	263

Table 5-3 (cont.)

Eqn. No.	Predictor X	Sex	A	B	E	r^2	N
59	Length of upper ramus (UM)	M	-1.07	1.33	2.89	0.9983	128
60		F	9.77	1.27	3.13	0.9925	75
61		U	6.98	1.27	3.64	0.9976	69
62		TOT	3.30	1.30	3.50	0.9968	269
63	Length of 4th premaxillary alveolus (PM4L)	M	85.54	19.62	12.64	0.9633	145
64		F	52.49	26.21	12.56	0.7241	74
65		U	51.12	27.06	16.07	0.9379	59
66		TOT	82.40	20.71	16.21	0.9216	278
67	Width of 4th premaxillary alveolus (PM4W)	M	99.82	20.00	10.98	0.9724	145
68		F	69.86	26.86	10.00	0.8251	74
69		U	69.43	26.97	13.63	0.9553	59
70		TOT	96.16	21.17	13.94	0.9421	278
71	Length of 5th maxillary alveolus (M5L)	M	73.86	17.25	12.53	0.9635	147
72		F	51.91	21.23	12.67	0.7549	75
73		U	53.91	21.19	18.57	0.9173	60
74		TOT	72.67	17.93	15.68	0.9266	282
75	Width of 5th maxillary alveolus (M5W)	M	102.53	16.36	11.89	0.9670	148
76		F	64.66	23.66	9.84	0.8522	75
77		U	78.45	21.66	15.84	0.9399	60
78		TOT	99.91	17.31	15.02	0.9324	283
79	Mandible length (ML)	M	19.68	0.75	3.95	0.9952	144
80		F	7.21	0.81	2.31	0.9953	74
81		U	11.58	0.78	3.34	0.9972	73
82		TOT	16.67	0.76	3.72	0.9950	291

Table 5-3 (cont.)

Eqn No.	Predictor X	Sex	A	B	E	r^2	N
83	Length of mandibular symphysis (LMS)	M+F	48.14	3.83	7.32	0.9772	218
84		U	18.33	4.50	8.14	0.9835	73
85		TOT	38.91	4.04	8.53	0.9737	291
86	Width of mandibular symphysis (WMS)	M	71.82	4.24	9.81	0.9701	144
87		F	32.52	5.84	9.68	0.9361	74
88		U	11.17	6.64	13.65	0.9535	73
89		TOT	62.54	4.65	15.48	0.9135	291
90	Dentary length (DL)	M+F	-0.97	1.23	3.79	0.9936	217
91		U	5.21	1.19	2.76	0.9977	71
92		TOT	1.21	1.22	3.71	0.9945	288
93	Dentary width (DW)	M+F	84.80	9.83	10.88	0.9471	217
94		U	25.47	15.09	14.49	0.9476	73
95		TOT	72.21	10.86	15.23	0.9137	290
96	Width across surangulars (WSR)	M	54.05	1.43	9.77	0.9795	147
97		F	42.07	1.59	7.89	0.9348	75
98		U	27.89	1.73	10.66	0.9768	87
99		TOT	48.30	1.50	11.50	0.9657	309
100	Length of lower ramus (LM)	M+F	-5.49	1.54	4.42	0.9926	194
101		U	4.87	1.46	4.83	0.9946	51
102		TOT	-2.10	1.52	4.68	0.9926	245
103	Length of 1st dentary alveolus (D1L)	M	79.07	20.75	10.86	0.9538	141
104		F	65.01	24.07	11.71	0.7599	74
105		U	51.71	25.65	15.27	0.8704	46
106		TOT	77.37	21.29	12.50	0.9162	261

Table 5-3 (cont.)

Eqn. No.	Predictor X	Sex	A	B	E	r^2	N
107	Width of 1st dentary	M	82.30	21.48	9.49	0.9647	141
108	alveolus (D1W)	F	69.71	24.42	9.54	0.8408	74
109		U	62.34	24.70	14.53	0.8827	46
110		TOT	80.10	21.97	10.89	0.9364	261
111	Length of 4th dentary	M	73.89	20.44	13.33	0.9304	141
112	alveolus (D4L)	F	58.40	23.63	11.42	0.7718	74
113		U	44.23	25.59	14.16	0.8885	46
114		TOT	71.48	21.03	13.43	0.9032	261
115	Width of 4th dentary	M+F	99.94	20.19	12.14	0.9219	215
116	alveolus (D4W)	U	56.36	29.24	14.65	0.8807	46
117		TOT	96.36	20.91	13.48	0.9025	261
118	Length of 11th dentary	M	73.75	19.16	10.27	0.9587	141
119	alveolus (D11L)	F	22.97	27.49	12.20	0.7398	74
120		U	52.73	21.70	13.60	0.8841	43
121		TOT	70.43	19.68	12.18	0.9199	258
122	Width of 11th dentary	M	111.08	18.61	11.34	0.9496	141
123	alveolus (D11W)	F	73.45	27.62	12.18	0.7404	74
124		U	75.11	26.28	11.62	0.9154	43
125		TOT	108.24	19.40	12.92	0.9095	258

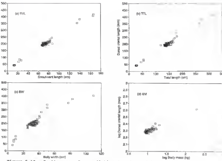
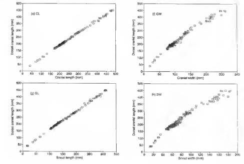


Figure 5-10 Scattergrams for predicting dorsal cranial length for *Crocodylus novaeguineae* from other body or skull measurements.



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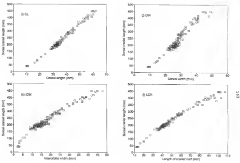

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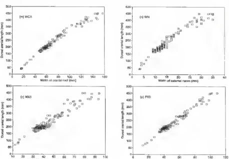

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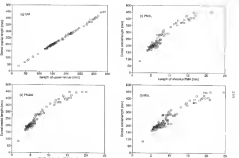

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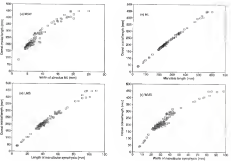

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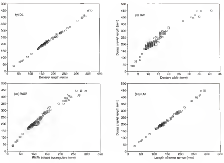

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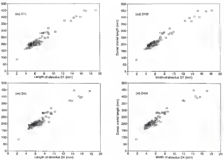

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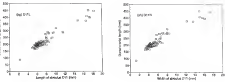


Figure 5-10 (cont.).

Predicting Body Size From DCL

The use of DCL as an independent variable to predict body size measurements may be accomplished by the regression coefficients in Table 5-4. The observed shrinkage between freshly killed C. novaeguineae and their cleaned, dried skulls was approximately 4% DCL, which conforms with earlier reports (Montague, 1984b). Thus, a correction factor of 1.04 DCL should be used for dried skulls prior to estimating body sizes.

If DCL is an estimated value derived from one of the preceding isometric predictors (SL, CL, UM, ML, DL, LM), the standard error of the final regression estimate (E_3) is calculated as follows: $\sqrt{[(b_2E_1)^2+E_2^2]}$, where b_2 is the slope of the second equation, and E_1 and E_2 are the error estimates from the first and second equations, respectively (Webb and Messel, 1978).

The largest live male and female in this study measured 313 and 265 cm total length (TTL), respectively; while the largest male skull measured 485 mm DCL (473 mm pre-shrinkage estimate) which would equate to a TTL estimate of 360 cm. The maximum verified sizes (TTL) of southern form C. novaeguineae are 335 cm for males (Montague, 1984b) and 265 cm for females (above). The form of this species that occurs in northern New Guinea attains larger known TTLs: males = 347 cm; females = 305 cm (Hall, CHAPTER 3).

Table 5-4. Linear regression coefficients for predicting body size measurements of Crocodylus novaeguineae from dorsal cranial length (DCL) by the equation Y = A + BX, where A is the Y intercept, B the slope. Equations are expressed separately by gender (M = males, F = females) where they differed by sex ($P < 0.05$), and are combined (M+F) where no such differences were detected. U = sex unknown. TOT = total sample. E = standard error of the regression model, r^2 = coefficient of determination. N = sample size.

Eqn No.	Predicted value Y	Sex	A	B	E	r^2	N
126	Snout-vent length (SVL)[A]	M	-7.03	0.41	2.70	0.9603	126
127		F	-1.94	0.38	2.53	0.9004	70
128		U	1.25	0.29	0.92	0.9286	27
129		TOT	-3.96	0.39	2.64	0.9866	223
130	Total length (TTL)[A]	M	-4.71	0.77	5.04	0.9605	126
131		F	11.89	0.67	5.91	0.8726	72
132		U	-0.03	0.66	1.02	0.9826	27
133		TOT	-3.88	0.76	5.40	0.9852	225
134	Belly width (BW)[A]	M+F	-18.53	0.26	3.29	0.8117	206
135		U	-3.23	0.16	1.75	0.9832	12
136		TOT	-12.54	0.23	3.56	0.8280	218
137	LOG_{10} Body mass (BM)[B]	M+F	-6.32	3.20	0.05	0.8068	189
138		U	-4.07	1.74	0.08	0.9141	6
139		TOT	-6.81	3.41	-0.06	0.9763	195

[A] – Cm; DCL in mm.

[B]A – Kg. using LOG_{10} DCL as a predictor.

Sexual Dimorphism

Sexual dimorphism was observed in snout-vent length (SVL), TTL, and in 21 of 32 skull attributes (Table 5-5). These differences varied from slight to pronounced at the size of the largest female in this study (352 mm DCL). Male *C. novaeguineae* of that size DCL possess a longer SVL, TTL, cranial length (CL), and mandible length (ML), but have a shorter premaxillary symphysis length (PXS) and upper ramus length (UM) than females. Males also exhibit greater widths with respect to their cranium (CW), snout (SW), orbit (OW), interorbit distance (IOW), cranial roof (WCR), external nares (WN), mandibular symphysis (WMS), and distance across the surangulars (WSR). However, the most obvious evidence of dimorphism exists in regard to dentition in which the alveoli PM4, M5, D1, D4, and D11 are conspicuously more robust in males. The alveoli PM4, M5, D1, and D4 are pseudo-canines in the genus *Crocodylus*. Their dimorphic character in this species suggests a possible relation to the social ordering of adult males that compete for territories and access to breeding females.

Changes in the directional rates of skull growth indicative of sexual dimorphism commence in *C. novaeguineae* at about 100 cm TTL. Females begin to exhibit proportionally longer skulls than males of equivalent TTL; however, differences in the proportional widths of skulls are not manifest until a TTL of about 180 cm is attained.

Table 5-5. Body size and skull attributes (see Table 5-1) exhibiting sexual dimorphism when used as predictors of dorsal cranial length (DCL) for *Crocodylus novaeguineae*. Comparisons are of estimated sizes (mm)[a] for animals the size of the largest female in the study (DCL = 355 mm). Significance levels are inclusive of all individuals in the regression models (see Table 5-3).

Attribute	Predicted size Female	 Male	Percent difference	Significance level
SVL	137.1	139.3	+1.6	$P < 0.005$
TTL	261.1	270.4	+3.6	$P < 0.0005$
CL	371.9	376.8	+1.3	$P < 0.05$
CW	171.3	190.2	+11.0	$P < 0.0001$
SW	124.2	135.1	+8.8	$P < 0.0001$
OW	38.0	38.6	+1.6	$P < 0.05$
IOW	31.8	33.4	+5.0	$P < 0.005$
WCR	111.0	114.7	+3.3	$P < 0.005$
WN	25.1	25.8	+2.7	$P < 0.05$
PXS	84.8	80.0	-5.7	$P < 0.05$
UN	269.5	265.5	-1.5	$P < 0.05$
PM4L	11.43	13.58	+18.8	$P < 0.05$
PM4W	10.50	12.61	+20.1	$P < 0.05$
M5L	14.14	16.12	+14.0	$P < 0.0005$
M5W	12.14	15.25	+25.6	$P < 0.005$
ML	425.7	443.1	+4.1	$P < 0.005$
WMS	54.7	66.1	+20.8	$P < 0.0001$
WSR	194.9	208.4	+6.9	$P < 0.0001$
D1L	11.92	13.15	+10.3	$P < 0.005$
D1W	11.56	12.56	+8.7	$P < 0.05$
D4L	12.42	13.61	+9.6	$P < 0.05$
D11L	11.97	14.52	+21.3	$P < 0.05$
D11W	10.09	12.95	+28.3	$P < 0.01$

[a] - SVL and TTL size in cm.

Size-Age Relations

Growth estimates for male *C. novaeguineae* to age nine and females to age 13 (Hall, CHAPTER 3) were fitted to a modified Richards curve (Brisbin et al., 1986) to derive growth models for predicting size-age relations. Initial models were calculated from known maximum sizes of 335 and 265 cm TTL for males and females, respectively, as final asymptote size parameters. These equations were rerun to develop a second model set using the predicted maximum size estimate of 360 cm TTL for males (above) and with a value of 285 cm TTL for females. This latter value was obtained by using a proportional size ratio estimate as for known sizes (265/335 x 360). A third set of growth models were calculated using a Brody curve (Gates and Dahm, 1989), another modification of Richards curve, with final asymptote sizes as in the first model pair (Fig. 5-11).

Although the Brody growth model closely paralleled the female model with known asymptote size, it considerably underestimated the comparable model for males. Regardless of gender, growth forms diverged at about age 15 for all models. Although these models may approximate mean growth for wild *C. novaeguineae*, they are speculative and their accuracy is unknown. However, it is apparent that considerable error could result from attempts to age animals longer than 210 cm that are beyond the point of model divergence.

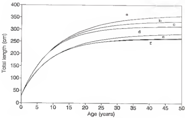


Figure 5-11. Growth curves for Crocodylus novaeguineae. Data fitted for (a) estimated maximum male size with a modified Richards curve, (b) maximum known male size with a modified Richards curve, and (c) maximum known male with a Brody curve. Curves (d)-(f) as preceding, but for females.

Gender Classification

The original relative growth data set incorporated a total of 27 ratio indices for a complete skull. These included 15 cranial and 12 mandibular aspects of growth (Table 5-6).

There was considerable overlap among canonical coefficients in the relative growth data set. Nevertheless, initial discriminant analysis (DISCRIM) results were highly promising (e.g., overall apparent error rate [AER] = 3.6% misclassification with a complete skull), but alarmingly illusory as the crossvalidation true error rate [TER] was 44.8%. When the same data set was evaluated by classification tree analysis (CART) the resulting AER (26.1%) provided a realistic estimate of the TER (28.7%). The best overall discrimination resulted from CART analysis of the cranium only, where a subset of only two cranial attributes (relative width of snout [RWST] and relative length of cranial roof [RLR]) were selected by the model for classification of gender (Fig. 5-12).

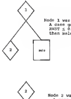
The wide disparity between AERs and TERs was a consistent feature of DISCRIM, while CART results yielded error rates that such more closely paralleled each other. Whether a complete or partial skull was analyzed, fewer observations were misclassified using CART methodology than with DISCRIM when TERs are taken into account. Regardless

Table 5-6. Comparison of predictive models for gender of *Crocodylus novaeguineae* using discriminant analysis (DISCRIM) and classification tree analysis (CART). AER = apparent error rate, TER = true error rate determined by crossvalidation (see METHODS). N = sample size.

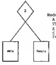
SKULL TYPE	GENDER	METHOD DISCRIM AER	 TER	 N	 CART AER	 TER	 N
Complete skull	M	0.0442	0.2566	113	0.2532	0.2727	154
	F	0.0278	0.6389	72	0.2763	0.3158	76
	M+F	0.0360	0.4478	185	0.2609	0.2870	230
Cranium[A] only	M	0.2033	0.2927	123	0.1503	0.1765	153
	F	0.0811	0.3514	74	0.3553	0.4211	76
	M+F	0.1422	0.3220	197	0.2183	0.2576	229
Mandible[B] only	M	0.3391	0.4087	115	0	0	145
	F	0.1667	0.3750	72	1	1	74
	M+F	0.2529	0.3918	187	0.3379	0.3379	219

[A] - Variables RCW, RLST, RWST, ROL, ROW, RWI, RLR, RWN, RMXS, RPXS, RLLMR, PM4LR, PM4WR, M5LR, M5WR

[B] - Variables RLSS, RWSS, RLD, RWD, RWM, RLLMR, D1LR, D1WR, D4LR, D4WR, D11LR, D11WR



Node 1 was split on variable RWST. A case goes left to node 2 if RWST ≤ 0.496. If RWST > 0.496, then male.



Node 2 was split on variable RLR. A case goes left if RLR ≤ 0.694. Thus, if RWST ≤ 0.496 and RLR ≤ 0.694, then male, if RWST ≤ 0.496 and RLR > 0.694, then female.

Figure 5-12. Variable classification tree produced from CART methodology.

of the method used, better gender classification resulted from use of the cranium than the mandible alone.

Subsequent examination of the original DISCRIM data set by stepwise discrimination analysis (STEPDISC) resulted in reduced model sizes consisting of a maximum of four variables (RWST, RLR, relative upper ramus length (RLUMR), relative mandibular symphysis width (RWSS) (Table 5-7). Construction of a series of 'best fit' models by DISCRIM using the STEPDISC selected variables gave such improved results and better correlation among AERs and TERs that approximated the CART 'best fit' model consisting of the variables RWST and RLR (Table 5-8).

Relative Growth Patterns

Relative growth patterns for the skull of Crocodylus novaeguineae are shown in Figure 5-13. Growth is characterized by three general stages: (I) a hatchling phase, (II) a juvenile through middle-aged adult phase, and (III) an old-aged adult phase.

Stage I is maintained through most of the first year of growth until a DCL of 60-70 mm (40-50 cm TTL) is attained. In this stage, the preorbital region of the skull is characterized by a relatively short, robust snout with comparatively narrow external nares. The orbital region features enormously enlarged orbits (primarily in relative width) with correspondingly narrow interorbital width; while

Table 5-7. Stepwise discriminant analysis results indicating relative growth variables and associated P values for 'best fit' predictive models of gender for *Crocodylus novaeguineae*

SKULL TYPE	N	STEP 1 RWST	STEP 2 RLUMR	STEP 3 RLR	STEP 4 RWSS
Complete skull	185	0.0001	0.0002	0.0006	0.0096
Cranium only	197	0.0001	0.0001	0.0025	N/A
Mandible only	219	N/A	N/A	N/A	0.0001

Table 5-8. Comparison of 'best fit' predictive models of gender for *Crocodylus novaeguineae* using stepwise discriminant analysis (STEPDISC - Table 5-7) and classification tree analysis (CART). AER = apparent error rate, TER = true error rate determined by crossvalidation (see METHODS). N = sample size

		METHOD					
SKULL TYPE	GENDER	STEPDISC AER/TER		N	CART AER/TER		N
Complete[A] skull	M	0.2521	0.2521	119			
	F	0.2162	0.2432	74	Below model only		
	M+F	0.2342	0.2477	193			
Cranium[B] only	M	0.3200	0.3520	125	0.1503	0.1765	153
	F	0.1600	0.1867	75	0.3553	0.3553	76
	M+F	0.2400	0.2693	200	0.2183	0.2358	229
Mandible[C] only	M	0.3034	0.3034	145			
	F	0.3649	0.3649	74	Above model only		
	M+F	0.3342	0.3342	219			

[A] - Variables RWST, RLUMR, RLR, RWSS.
[B] - Variables RWST, RLUMR, RLR for STEPDISC; RWST, RLR for CART.
[C] - Variable RWSS.

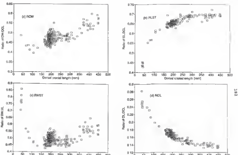
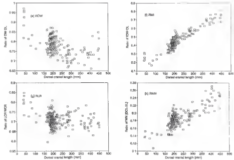


Figure 5-13. Scattergrams of relative growth ratios for Crocodylus novaeguineae



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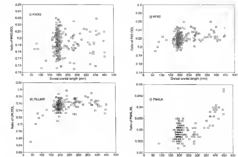

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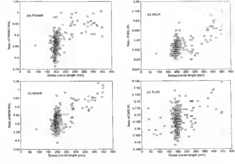

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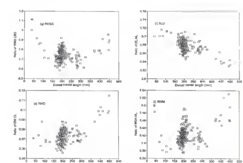

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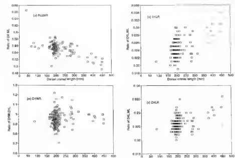

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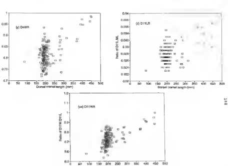

Figure 5-13 (cont.)

in the postorbital portion of the skull, the cranial roof assumes the shape of a convex trapezoid in contrast to the concave appearance in subsequent growth stages.

The change from stage I to stage II skull growth is very abrupt, paralleling the 'saltatory ontogeny' model proposed by Balon (1984). The secondary stage is a protracted phase exhibited until animals reach a DCL of about 350 mm (roughly 260 cm TTL). It is in this stage that the crocodilian skull acquires the proportions of generalized morphology typically associated with the species. The snout becomes relatively long and slender, there is an increase in width in external nares and interorbital distance, the orbits are much reduced in size from stage I, and the cranial roof becomes a concave-shaped trapezoid for the duration of life.

By virtue of size, stage III growth consists predominantly of large adult males and excludes all but the largest size females. In stage III the directional rates of growth undergo another transformation. As the skull length asymptote is approached, a reversal toward the hatchling stage I phase is manifest with respect to the skull becoming increasingly more robust while the snout becomes proportionally shorter. Thus, an individual may exhibit identical relative growth ratios for a given attribute within its life span, but at different stages of growth and at widely differing ages. Hence, some independent measure of size, such as DCL, must be incorporated to lend meaningful interpretation to relative growth data.

Discussion

Relative Growth

Relative growth indices are a useful way to chronicle ontogenetic patterns of growth and to segregate morphologically similar species (Dodson, 1975; Simpson, 1980; Hall, 1989). Such indices in this study reveal three distinct stages of skull growth in C. novaeguineae: a hatchling phase (I), a juvenile to middle-aged adult phase (II), and an old-aged adult phase (III).

Saltatory ontogeny (sensu Balon, 1984) is a series of near spontaneous changes in form and function that lead to 'threshold' states between the organism and its environment. This life-history model is a hierarchical system of intervals based on evolutionary opposite trends between altricial (generalist) and precocial (specialist) forms. Examples include threshold responses from photophobia to phototaxis and from endogenous to exogenous feeding in early ontogeny. The abrupt shift in patterns exhibited by hatchling C. novaeguineae from stage I to stage II relative skull growth mimics a saltatory response. Hatchling crocodilians possess a residual embryonic yolk reserve that continues to provide nutrients for growth in the early posthatching period (Whitehead, 1990). In addition to the depletion of yolk reserves during the stage I phase of hatchling cranial growth, there is a concomitant dietary shift from an invertebrate prey base toward a gradual inclusion of vertebrate items that form the mainstay of forage for older animals. This is evidenced by structural modifications of the skull whereby hatchlings are principally visually oriented versus the diminution of the orbital region and expansion of the external nares throughout growth stages II and III, inferring greater reliance on olfactory prowess in older animals rather than on visual acuity. The shift from stage II to stage III skull growth is not as rapid and pronounced as from stage I to stage II, but it is in this stage that animals attain the size and are afforded the massiveness and strengthening of the skull through increased robustness to feed on the largest vertebrate prey items available.

Gender Classification

The correctness of classification rates of biological observations by discriminant analysis are strongly influenced by group sample sizes and the distributional overlap among groups. When overlap is high, as in this study, sample sizes must be increased with respect to the number of variables to provide a given level of precision. Williams et al. (1990) recommend that sample sizes be at least two times the number of variables to be measured when among group overlap is low and substantially more as the overlap increases. Sample sizes in this study for a complete skull ranged from approximately four times the variable number for the general DISCRIM model (Table 5-6) to 60 times that number for the 'best fit' model (Table 5-8). As noted earlier, CART methodology maximizes the number of available observations since it treats missing value data, whereas DISCRIM does not. This feature, plus its ease of use and interpretation, makes CART preferable to DISCRIM for classification purposes. More importantly, in this study CART provided consistently lower TERs that gave more realistic assessments of model AERs than did DISCRIM. However, the choice of methodology is not so clear cut when one compares 'best fit' models since DISCRIM performed nearly as well as CART in that regard, although it entailed the use of three more attributes (LMS, UM, WHS) than the latter method (both used DCL, LCR, SL, SW and WCR).

The fact that the cranial roof and snout were selected as predictive variables for the classification of gender in both the DISCRIM and CART 'best fit' models suggests that better results might be obtained through the addition of other measures of the shapes of those variables. Post- and preorbital attributes that may prove of use in further investigation are as follows: (1) the midpoint width of the cranial roof, and (2) the intersuprafenestral width of the parietal; plus, three other measurements of the snout

These latter include (3) the mid-snout width (at the level of the 5th maxillary alveoli), (4) the width at the point of anterior snout constriction (posterior to the external nares), and (5) the maximum premaxillary snout width (at the midpoint of the external nares).

Size-Age Relations

Attempts at aging crocodilians usually involve capture-recapture studies (McIlhenny, 1934, 1935; Lawson, 1972; Staton and Dixon, 1975; Webb, 1977; Gorzula, 1978; Webb and Messel, 1978; Webb et al., 1978; Chabreck and Joanen, 1979) or observed growth in captivity (Cott, 1961, Montague, 1982). Graham (1968) employed growth annuli in the dentary bone and the weight of the eye lens to determine the age of a sample of harvested C. niloticus. However, those methods provided less than satisfactory results. Subsequently, Hutton (1986, 1987c) reported that cross-sections of nuchal scutes from that species provided better resolution and a more reliable method of aging. However, as noted above, considerable margin for error in aging crocodilians still exists. Hutton's (1986) study provides the most rigorous evidence to date of the magnitude of error resulting from attempts to age these reptiles. In that study, the range of errors of individual estimates were about 22% for known-aged crocodiles above age 13, while errors of mean estimates ranged from 15% for 13 year old animals to 9% for a 46 year old individual. Errors are likely to be greater in females due to lines of arrested growth resulting from reabsorption of calcium from ossified areas during the reproductive cycle (Wink and Elsey, 1986). Thus, use of the growth curves in this study (Fig. 5-11) will likely produce spurious results for all but the youngest age classes.

The teeth of certain mammalian species exhibit growth annuli and have long been used for aging purposes (e.g., Marsh, 1981). Crocodilian teeth also possess growth zones (Poole, 1961; Johnston, 1979). However, crocodilians have polyphyodont dentition characterized by replacement in irregular sequence and at irregular intervals (Edmund, 1962). These properties render crocodilian teeth unsuitable for aging purposes. I believe, though, that the size of dental alveoli may prove to be a useful indicator of age in crocodilians since growth of an alveolus appears to be continual, except in rare pathological conditions (Hall, 1985a). Further investigation along these lines is required.

Summary

Size estimates of harvested C. novaeguineae may be derived with a high degree of accuracy from a complete skull or from fragments thereof. Allometric coefficients are provided for the estimation of dorsal cranial length (DCL) from body and skull attributes and for the determination of body size attributes from DCL. Best estimates of DCL are obtained from the use of cranial attributes SL (snout length), CL (cranial length), UM (upper ramus length) and mandibular attributes ML (mandible length), DL (dentary length), LM (lower ramus length).

Sexual dimorphism is subtle but significant with respect to body size (SVL, TTL) and 21 of 32 skull attributes. Differences among sexes ranged from 1.3% to 28.3% for a given attribute at the size of the largest known female *C. novaeguineae* and were most pronounced in the relative sizes of dental alveoli.

Relative growth indices reveal three distinct stages of skull growth. Stage I is characteristic of hatchling crocodiles, stage II of juvenile through middle-aged adults, and stage III of large elderly adults (principally males). Stage 1 growth abruptly shifts to stage II at about 60-70 mm DCL and mimics a saltatory ontogenetic response. The shift from stage II to stage III occurs at about 350 mm DCL and is less abrupt than stage I. Stage III is characterized by a reversal in directional rate of growth toward that found in stage 1 where the relative snout length is decreased and measures of skull width increase.

The use of relative growth indices for the skull of *C. novaeguineae* provides a reasonable means of determining the gender of unknown sex animals by classification through multivariate discriminant analysis (DISCRIM) or through non-parametric binary tree classification (CART). CART methodology provided consistently lower apparent error rates (AERs) that better correlated with crossvalidation true error rates (TERs) than those obtained by DISCRIM. However, when 'best fit' models were selected from variables used in general classification models, DISCRIM performed nearly as well as CART. Error rates were invariably greater for females than males regardless of the method or model employed. Suggestions are made for the possible improvement of classification results through the addition of other measures of predictive attributes used by the 'best fit' models.

In conclusion, the use of hunter harvested skulls of *C novaeguineae* can provide valuable demographic insights to the size structure and sex composition of populations from remote, difficult access locations that are otherwise unlikely to be obtained. This knowledge will offer a cost-effective method of monitoring population trends of future harvests and enhance the management potential for achieving optimal resource use.

CHAPTER 6
CONCLUSION

The potential for drawing demographic inferences of crocodilian populations from seemingly disparate sources and on hitherto poorly known aspects of their biology was investigated in this study. The patterns of harvest, reproduction, and skull morphometry were examined variously for one or more of three species: populations of New Guinea (*Crocodylus novaeguineae*) and saltwater (*C. porosus*) crocodiles from Papua New Guinea (PNG), plus populations of American alligators (*Alligator mississippiensis*) from the states of Florida and Louisiana, USA.

Historically, tens of millions of crocodilians have been killed as vermin or for their commercial value. Annual worldwide trade is presently estimated to be between one and two million hides, of which perhaps 70% or more are illegal (Brazaitis, 1987). Hence, accurate harvest data are seldom available for interpretation and such data as exist often are based on small samples that result from the interception of confiscated hides (e.g., Rebêlo and Magnusson, 1983). A notable exception is the study of Taylor and Neal (1984) based on Louisiana alligator harvests.

My analysis of 1969-1980 harvest data for PNG crocodile populations (CHAPTERS 2 and 3) indicated that substantial numbers of both species were continuing to be harvested on an apparent sustained yield basis in spite of several decades of previously unregulated exploitation. Although management controls were instituted in 1969, the crocodile skin trade remained largely in the hands of expatriates until independence was attained in 1975. Following that, collaborative efforts were made with the Food and Agricultural Organization of the United Nations (FAO) to restructure the industry so that indigenous landowners became the focal beneficiaries of the resource (Bolton and Laufa, 1982). During these years of regulated harvest a tremendously large harvest data base was developed; unfortunately, the compilation was lacking and much was left to desire in the type of data generated. Nonetheless, it was possible for me to reconstruct species-specific harvest size and sex compositions on those data to gain demographic insights to the structures of previous populations. While this entailed the use of some rather liberal assumptions, the process also afforded the opportunity to rectify data collection procedures for future harvests to provide management authorities with a more instructive format on which to base regulatory decisions. Those reforms were instituted and subsequent monitoring indicates that population recovery of these species is continuing satisfactorily (Hollands, 1987).

Even for the best studied crocodilian species, A. mississippiensis, the understanding of demographic parameters often amounts to blatant speculation (Abercrombie, 1989). Speculative or not, the analysis in CHAPTER 3 offers a method of estimating cumulative and age-specific mortality rates from harvest returns and provides some insight as to what may be occurring (e.g., greatly higher mortality among harvested populations of C porosus than C. novaeguineae). Similarly, CHAPTER 4 outlines a simple but effective manner of accurately determining structures of nesting female crocodilian population segments. The inferential evidence on the effects of density-dependent nesting as a consequence of adult female size offers an intriguing hypothesis for the type of potential experimental manipulation advocated by Macnab (1983, 1985) for wildlife managers.

However, there is a more immediately applicable lesson from the demographic inferences of CHAPTER 4. This is that there is yet another line of independent evidence (see Montague, 1984; Cox, 1985; Hall and Johnson, 1987) indicating that the legislation enacted to protect crocodile brood stocks in PNG is less effective than originally intended. That the original act was drafted without benefit of adequate biological input is an important consideration

In the mid-1980's a crocodile management program modeled after the one designed in PNG was established in neighboring Irian Jaya (Cox, 1990). Having benefitted from the PNG experience, slot size limits on the trading of Irian Jayan crocodile skins were set at 25 to 46 cm commercial belly width (BW) as opposed to limits of 18 to 51 cm in PNG. Although not wholly effective, a 46 cm BW size limit (101 cm snout-vent length (SVL) equivalent) affords greater protection to nesting female _C. novaeguineae_ than does a 51 cm size limit (see Fig. 4-3). Serious consideration should be given to revising the slot size limits in PNG and to standardizing them with those in Irian Jaya. This would help thwart the possible transhipment of underalzed or oversized skins from Irian Jaya to PNG and simultaneously better fulfill the goals of the initial legislation on upper size trading limits.

The options available to management authorities responsible for the conservation of these resources may be strikingly different for as much economic and logistic reasons as for biological ones. The methodologies I offer for the assessment of demographic parameters of crocodilian populations should prove cost-effective for developed and developing nations alike. The use of hunter harvested (or illegal kill) skulls as a valuable demographic artifact (CHAPTER 5) will probably prove of greater benefit to developing tropical nations that are more constrained by logistic and economic considerations. An effective and inexpensive sampling program could easily be established in remote areas subject to hunter harvest for the collection of skull parts from culled animals. A skull provides a much better estimate of live animal size (SVL or total length) than does skin measure (higher r^2 value; see Table 5-1). At a minimum, a single bone from the lower jaw, the dentary, will suffice for use in determining sample size structures of harvests. A sex ratio interpretation for C. novaeguineae harvests may also be inferred with a reasonable degree of error, providing that the cranium is used for gender classification. Further study on this subject is required to refine the technique and to assess its applicability toward other species.

Following the termination of FAO input to the PNG crocodile skin industry much financial support for the maintenance of the program management has been derived from private sector commercial beneficiaries to supplement revenues from government sources. Whether there or in the USA, it is appropriate and vital that such contributions be made as a form of 'value-added' conservation (Hines and Percival, 1987). It is equally imperative that management agencies do not become fiscally undermined by governmental budgetary processes or compromised as a consequence of such sources and that they be able to maintain active and continual research components as part of their overall conservation planning.

APPENDIX A

LIST OF LICENSED CROCODILE SKIN EXPORTERS

Table A-1. Names and addresses of authorised crocodile skin exporters from Papua New Guinea (PNG) during 1969-1980, preceded by license number and followed by dates of documented activity and license status.

1	Horiuchi Trading Co. Ltd. 8 Mitoshirocho Kanda Chiyoda-ku Tokyo Japan 1969 1973 EXPIRED 1/74
2	Angenmeyer (Australasia) P L P O Box 86 Lae Morobe Province PNG 19[illegible] 1973 EXPIRED [illegible]74
3	Unknown
4	William John Besley Delta Stores Kikori Gulf Province PNG Unknown, EXPIRED
5	Jack Unknown P O Box 54 Daru Western Province PNG 1969 1972-1977 EXPIRED 8/77
6	Ernest C Kalaitzis (P N G) Pty Ltd P O Box 121 Port Moresby NCD PNG 1972 1980 ACTIVE
7	Bernard Beets P O Box 57 Daru Western Province PNG 1972 1972: EXPIRED 3/73
8	Unknown
9	George Craig P O Box 3 Daru Western Province PNG Unknown EXPIRED
10	Margaret Helen Brown Aramia Trade Store Balimo Western Province PNG 1969 1972 EXPIRED [illegible]
11	Unknown
12	Colin Charles Ryman Unknown
13	Unknown
14	Unknown
15	Unknown
16	Crest & Co Pty Ltd P.O. Box 437 Rabaul E. New Britain Prov PNG 1969 1973 EXPIRED 3/71
17	Unknown
18	Unknown
19	Iroom Dina Gadola Baimuru, Gulf Province PNG No exports: EXPIRED 3/71
20	Kee Hong Tang P O Box 139 Lae Morobe Province PNG 1969 1970: EXPIRED 3/73
21	Unknown
22	Unknown
23	Unknown
24	Unknown
25	Unknown
26	Gregory Beato Talasea W. New Britain Prov PNG No exports EXPIRED 7/71
27	Unknown
28	Unknown
29	Unknown
30	John Pupendable P O Box 6333 Port Moresby NCD PNG 1972 EXPIRED BY COURT ORDER 8/77
31	Kraus PNG P O Box 1381 Boroko PNG 1972 EXPIRED 9/73
32	Andersons and Co Pty Ltd. P O Box 1913 Melbourne 3001 Australia 1971-1978: EXPIRED 73
33	Unknown
34	Unknown
35	W B Bradbury P O Box 1187 Boroko NCD, PNG 1973-1978 CANCELLED 5/78
36	Berry Small Brown P O Box 11 Wau Morobe Province PNG No exports EXPIRED 11/73
37	Bjarne Koppersen P O Box 1333 Boroko NCD PNG No Unknown: EXPIRED 3/73
38	Luke Lahara P O Box 283 Kieta Bougainville PNG 1973: EXPIRED 10/74
39	Paddy Harve P O Box 53 Daru Western Province PNG No exports: EXPIRED 11/73
40	Gordon-Ubidy 31 Rue Jean-Pierre Baumann 76033 Paris France No Unknown EXPIRED 1/73
41	J T Crumble Pty Ltd P O Box 1983 Boroko NCD PNG 1973 EXPIRED 2/79

Table A-1 (cont.)

[illegible] James Murray Wilson
Vowega Corp Pty Ltd.
Box 7[illegible]
Lae, Morobe Province PNG
1977 EXPIRED 1/77

[illegible] Unknown

[illegible] Unknown

[illegible] Arahal C Kalimba
P.O. Box [illegible]
Angoram E Sepik Prov PNG
1978 [illegible]: ACTIVE

[illegible] Kevin William Thomas
P.O. Box [illegible]
Wewak E Sepik Prov PNG
No exports: EXPIRED 5/77

[illegible] Mikosel Yaura
P.O. Box [illegible]
Hera Southern Province PNG
1976-1977 1977 ACTIVE

[illegible] Ambus Mersah
Sub-provincial Office
Ambunti E Sepik Prov PNG
[illegible] ACTIVE

[illegible] William Kisbera
Korogwe Village
P.O. Box [illegible]
Angoram E Sepik Prov PNG
1977: ACTIVE

[illegible] Andrew Lowe Garoia
Tobona Village
Kerema Gulf Prov PNG
1976-1977: ACTIVE

[illegible] Murae Brothers
P.O. Box [illegible]
Wewak ESP PNG
No exports: EXPIRED 6/77

[illegible] Paul Henry Cirone
P.O. Box 76
Port Moresby [illegible] PNG
No exports: EXPIRED 9/77

[illegible] Dept of Primary Industry
P.O. Box 2417
Konedobu NCD PNG
1976-77 ACTIVE

[illegible] Sepik United Skin Buyers
Wewak E. Sepik Prov PNG
1976-1977: EXPIRED 1/77

[illegible] P N G Export
P.O. Box 93
Goroka Eastern Highlands Prov PNG
1976-1977 ACTIVE

[illegible] Lean Brothers
P.O. Box [illegible]
Angoram E Sepik Prov PNG
1976: EXPIRED 1/77

[illegible] [illegible] Hostel
c/o Wildlife Division
P.O. Box [illegible]
Kikori Gulf Province PNG
1977 1977: ACTIVE

[illegible] Teddy Pree
P.O. Box 7[illegible]
Lae Morobe Province PNG
No exports: EXPIRED 11/77

[illegible] Wonel Pty Ltd
P.O. Box 1
Manus Manus Province PNG
1976 1977 EXPIRED 7/77

[illegible] Laki Trading
P.O. Box 4
Daru Western Province PNG
1976-1977: EXPIRED 4/77

[illegible] Stafford R.J. Arnold
Arnold Trading
Daru, Western Province PNG
1977 EXPIRED 7/77

[illegible] Papuan [illegible] Business Group
Kerema Gulf Province PNG
Exported thru DPI: EXPIRED 9/77

[illegible] Barthol Moran
P.O. Box [illegible]
Angoram E Sepik Prov PNG
1977 ACTIVE

[illegible] Joseph [illegible]
P.O. Box 1984
Lae Morobe Province PNG
No exports: EXPIRED 11/77

[illegible] Wildlife Division
P.O. Box 2585
Konedobu NCD PNG
1976-1977 ACTIVE

[illegible] Gabriel [illegible] Wasebo
Wanamo Village
Baimuru Gulf Province PNG
1976-1977 ACTIVE

[illegible] Andrew Kenga
P.O. Box [illegible]
Popondetta Northern Prov PNG
No exports: EXPIRED 7/77

[illegible] Wododo (Manus) Ltd
P.O. Box [illegible]
Lorengau Manus Province PNG
1977 ACTIVE

[illegible] Peter Sisi
P.O. Box [illegible]
Angoram E Sepik Prov PNG
No exports: EXPIRED 8/77

[illegible] Thomas Arthur Nybers
P.O. Box 7
Daru Western Province PNG
1977 EXPIRED 8/77

[illegible] Laki Trading
P.O. Box [illegible]
Wewak ESP PNG
1977 (Dec) ACTIVE

[illegible] Peter DeTamul
Mim Village
Lake Murray Western Prov PNG
No exports: ACTIVE

Table A-1 (cont.)

8 Bergeret Shan
P.O. Box 520
Lae Morobe Province PNG
1988: CANCELLED BY COURT ORDER

84 Edward Mbon Bours
Tobes Village
Weiatua Gulf Province PNG
No exports: ACTIVE

8 Geoffrey Ling
Rabaul E. New Britain Prov. PNG
1978-1988: ACTIVE

8 Erel Itimo (Petoduk Business Group)
Petoke Village
Pt. Southern Province PNG
No exports ACTIVE

88 Nadong Isana (Bilaba Business Group)
Petoke Western Province PNG
No exports ACTIVE

88 Angoram Angati (Oambe Business Group)
Bomaet Western Province PNG
No exports ACTIVE

88 R.C. Galatean Pty. Ltd.
P.O. Box 890
Rabaul E. New Britain Prov. PNG
1978-1988: ACTIVE

90 Bullimore Pty Ltd
P.O. Box 8881
Morobe MCB PNG
1988-1988: ACTIVE

88 Maurel E.H. Chang
P.O. Box 1080
Morobe MCB PNG
1988-1988: ACTIVE

88 Simon Bosai
Unknown
No exports APPLICATION CANCELLED

88 Matthew Aitarepi
Laas Village c/o DPI
Ambunti Sub-district E. Sepik Prov PNG
No exports ACTIVE

88 Madang Quality Exporters Pty Ltd
P.O. Box 444
Madang Madang Province PNG
1988: ACTIVE

90 100 Feet (Yamano Holdings)
P.O. Box 818
Lae Morobe Province PNG
1988: ACTIVE

90 Tanagupa Pty Ltd
P.O. Box 1911
Morobe MCB PNG
1987 ACTIVE

88 Jacobs E. Edwards (Holdings)
P.O. Box 81
Lae Morobe Province PNG
1988-1988: ACTIVE

88 Lime Bay Province Pty Ltd
P.O. Box 8888
Morobe MCB PNG
1988: ACTIVE

90 Ryan Bergheimer
P.O. Box 1782
Morobe MCB PNG
No exports: ACTIVE

90 Jem Kenni
P.O. Box 25
Angoram E. Sepik Province PNG
No exports: ACTIVE

91 Otton Liliam
P.O. Box 8
Angoram E. Sepik Province PNG
1978 ACTIVE

88 Keith E. Urijan
Unknown
No exports: APPLICATION CANCELLED

91 Ludwig Schulze
Sepik Exporters
P.O. Box 82
Angoram E. Sepik Province PNG
1988 ACTIVE

94 Wewak Saving
P.O. Box 888
Wewak E. Sepik Province PNG
1988 ACTIVE

90 Sadol Saalie
c/o Arabeta Exporters
P.O. Box 878
Madang Madang Province PNG
No exports ACTIVE

88 Martin Bool
c/o Arabeta Trading Company
Madang Madang Province PNG
No exports ACTIVE

97 Sea Lilop (Lati Trading)
P.O. Box 8888
Morobe MCB PNG
1988 ACTIVE

90 Greg Mitchell
P.O. Box 188
Lae Morobe Province, PNG
1988: ACTIVE

94 Tom Sacca
c/o Kilemgie Division
P.O. Box 8070
Wabe Madang Province, PNG
1987: ACTIVE

APPENDIX B
SEX-BASED SIZE DISTRIBUTIONS OF
Crocodylus novaeguineae AND *C. porosus*

Table B-1. Sex-based distributions of *Crocodylus novaeguineae* and *C. porosus* according to commercial belly width size classes (see observed or estimated size class sex ratios in Tables 3-3 and 3-4). These data were transformed to age classes following the conversion factors in Tables C-1 and C-2, Appendix C.

	C. novaeguineae						*C. porosus*			
Belly width	Western Province		Sepik Provinces		Papua Region		New Guinea Region		Island Region	
(inches)	male	female	male	female	male	female	male	female	male	female
4	2105	1551	1935	1132	1129	1162	2155	1683	11	15
5	1105	4080	5515	8110	1840	2831	1865	3887	44	38
6	8313	8151	4601	3808	3531	1353	3330	1101	92	85
7	6851	5551	5308	3380	1625	1438	1115	1110	31	15
8	8135	3833	1815	1541	1840	3064	1501	1880	55	88
9	3350	1350	1144	1183	161	151	1218	1125	53	85
10	1603	1510	3873	3831	511	523	114	315	38	11
11	3123	1530	1105	545	383	301	815	458	55	51
12	1340	1133	3303	182	111	334	481	180	88	40
13	1165	1145	835	830	380	153	348	311	48	38
14	3383	3033	881	145	138	380	385	111	81	15
15	1441	515	1211	520	353	62	383	125	41	30
16	1400	838	3377	554	151	64	541	104	15	15
17	3111	565	1055	453	103	43	508	88	51	5
18	1283	833	3081	845	55	34	501	85	15	13
19	3053	851	881	181	35	13	185	88	34	14
20	1051	454	308	383	351	55	311	80	45	18
Totals	36888	41153	15155	42925	10815	12330	15405	10555	615	185
Sex ratio	0.88	0.81	1.02	0.58	1.05	0.55	1.02	0.55	0.51	0.43

APPENDIX C

CONVERSION FACTORS FOR SIZE TO AGE CLASS TRANSFORMATION IN *Crocodylus novaeguineae* AND *C. porosus*

Table C-1. Conversion factors for the transformation of size to age class in *Crocodylus novaeguineae*. Note that size is expressed in terms of commercial belly width (BW) size classes and reflects the fractional number of individuals for BW size class listed in Appendix B (e.g., Western Province male BW5 = 3109). For example, the number of 1-2 year old male *C. novaeguineae* from the Western Province shown in Table 3-6 was calculated by multiplying the sex-based distributions in Appendix B as follows: 10/11 (1709) + (3109) + 5/11 (5373) = 7105.

Age class (years)	Estimated size class (cm)	Conversion factor
		Male
1-1	≤ 57	1/11(BW1)
1-2	58 84	11/11(BW1) + (BW1) + 5/11(BW1)
2-3	11-108	6/11(BW6) + 10/31(BW7)
1-4	111-111	21/38(BW7) + 1/1(BW8)
1-1	111 150	1/1(BW1) + (BW1) + (BW11) + 1/1(BW11)
8-8	151-111	6/1(BW11) + (BW12) + 1/1(BW13)
1-1	111-111	3/1(BW11) + (BW11) + 1/7(BW11)
1-1	181-111	1/1(BW18) + (BW18) + (BW11)
1-1	197-206	(BW11) + (BW19)
9-11	107-211	(BW11)
		Female
0-1	≤ 11	1/11(BW1)
1-2	11-11	10/11(BW8) + (BW1) + 1/11(BW1)
1-1	11-11	10/11(BW1) + 1/11(BW7)
3-4	10 111	16/11(BW1)
8-9	118-120	11/11(BW1)
5-1	120-111	1/11(BW1) + (BW1) + (BW9)
9-7	111-154	(BW11) + 1/1(BW11)
1-1	115-160	2/1(BW11) + (BW11) + 1/1(BW11)
1-1	161-171	1/1(BW11) + (BW11)
1-11	111-186	(BW18) + 3/6(BW11)
10-11	111-114	1/1(BW11) + 1/1(BW11)
11-11	116-111	2/1(BW11) + (BW16) + 1/1(BW11)
12-13	111-111	6/1(BW11)
13-14	111-114	(BW11)

[a] The denominator represents the number of whole centimeters in the total length (TL) size class for an equivalent BW size class in Table 1-1 (e.g. - there are 11 cm for BW1). The numerator represents the number of centimeters per BW size class that apply toward the TL size class for an applicable age class shown in Table 1-8. In the above example male *C. novaeguineae* aged 1-1 years range from 11-11 cm TL and thus account for 11 of 11 cm from BW1 of Table 1-1 (58-11 cm) plus all of [illegible] from BW6 (11-11 cm) plus 5 of 11 BW from BW1 (11-11 cm)

Table C-2. Conversion factors for the transformation of size to age class in *Crocodylus porosus*. Note that size is expressed in terms of commercial belly width (BW) size classes and reflects the fractional number of individuals per BW size class listed in Appendix B (e.g., Papua Region male BW8 = 1064). For example, the number of 1-2 year old male *C. porosus* from the Papua Region shown in Table 3-9 was calculated by multiplying the sex-based distributions indicated in Appendix B as follows: 4/11 (1625) + (1064) + (761) + (522) + 3/11 (383) = 3042.

Age class (years)	Estimated size class (cm)	Conversion factor
		Male
0-1	≤ 75	(BW1) + (BW2) + (BW3) + 7/11(BW7)
1-2	76-111	4/11(BW7) + (BW8) + (BW9) + (BW10) + 3/11(BW11)
2-3	112-141	8/11(BW11) + (BW12) + 1/11(BW13)
3-4	142-172	10/11(BW13) + (BW14) + 8/11(BW15)
4-5	173-181	3/11(BW15) + (BW16) + 1/11(BW17)
5-6	182-211	6/11(BW17) + (BW18) + 3/11(BW19)
6-7	212-218	8/11(BW19) + (BW20)
		Female
0-1	≤ 75	(BW1) + (BW2) + (BW3) + 1/11(BW7)
1-2	76-107	4/11(BW7) + (BW8) + (BW9) + 1/11(BW10)
2-3	108-131	4/11(BW10) + (BW11) + 8/11(BW12)
3-4	132-145	2/10(BW12) + (BW13) + 2/11(BW14)
4-5	146-160	1/11(BW15) + 1/11(BW16)
5-6	161-170	8/11(BW15) + (BW16)
6-7	171-180	(BW17) + 4/11(BW18)
7-8	181-190	7/11(BW18) + 8/11(BW19)
8-9	191-215	3/11(BW19) + 1/10(BW20)
9-11	216-231	1/11(BW21)

[a] The denominator represents the number of whole centimeters in the total length (TL) size class for an equivalent BW size class in Table 3-1 (e.g., there are 11 cm for BW1). The numerator represents the number of centimeters per BW size class that apply toward the TL size class for an applicable age class shown in Table 3-8. In the above example, male *C. porosus* aged 1-2 years range from 76-111 cm TL and thus account for 4 of 11 cm from BW7 of Table 3-1 (71-79 cm) plus all of those from BW8 (80-91 cm), BW9 (91-100 cm) and BW10 (101-111 cm) plus 3 of 11 cm units from BW11 (111-118 cm).

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BIOGRAPHICAL SKETCH

Philip M. Hall was born on 13 June 1949 in Jamaica, New York, and subsequently raised in Levittown, New York. Trying not to let school interfere with his education, he left Hofstra University after one year in the elusive pursuit of some grander purpose. Following six years of Wanderjahren and several premature mid-life crises, he returned to the sphere of formal education at North Dakota State University in 1974. He received an A.A.S. in ecology and wildlife in 1975, and in 1976 graduated with a B.S. in zoology.

Shortly thereafter he embarked on broadening his cosmopolitan perspectives by joining the U.S. Peace Corps as a volunteer in a Nepalese fisheries development program. After two and a half years of introspective irreverancy and hitherto unrealized hardship and adventure he returned to the U.S.; whereupon, he was hopelessly maladjusted to the ostentatious ways of the developed, 20th century Western World. His fears of remaining a cultural and social pariah were soon tempered by the prospects of returning to the Third (and by then, normal) World. Following enrollment at the University of Idaho in 1979, he became a United Nations volunteer and went to Papua New Guinea where he spent two years as a crocodile biologist under contract to the Food and Agricultural Organization of the United Nations. Afterward, he returned to complete his degree program and received an M.S. in zoology from Idaho in 1983.

In the aftermath of several later life crises, he continued graduate study at Louisiana State University during 1985-1986 while intermittently researching alligators in southwestern Louisiana and working aboard Japanese trawlers and a Soviet processor in the Bering Sea and Gulf of Alaska.

In January 1987 he enrolled at the University of Florida where he is a candidate for the degree of Doctor of Philosophy, in the Department of Wildlife and Range Sciences, School of Forest Resources and Conservation.

During his years he has had the good fortune to have loved, known, and worked with many fine people and is fully appreciative of the privileges accorded him by his chance birthright in a democratically free, non-totalitarian society. Such is karma.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

F Wayne King

F. Wayne King, Chairman
Professor of Forest Resources
and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg

John F. Eisenberg
Katharine Ordway Professor of
Ecosystem Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

F.J. Mazzotti

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 1990

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